Joint remodelling and the evolution of the human hand

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INTRODUCTION

It is widely believed that a major breakthrough in hominid evolution was achieved by the firm establishment of cultural tool use and manufacture. However, amongst anthropologists it is usually tacitly assumed that the emergence of tool-making was unrelated to any spectacular advance in the functional anatomy of the hand (Oakley, 1972), for a belief in the essential primitiveness of the human hand is well entrenched in the literature (Sonntag, 1924). Jones (1949), who was a staunch protagonist of this view, considered that the great functional effectiveness of the hand was a measure of the elaboration of underlying nervous mechanisms; he stated 'when we look for remarkable specializations, or wonderful human adaptations as distinguishing our hands from the hands of monkeys and anthropoid apes, our search is rather a vain one'. Because of recent advances in our knowledge of primate evolution, and of the correlations between structure and function in the locomotor system, the time has come for a critical re-examination of this widely accepted view.

It was recognized by Landsmeer (1955) that the human hand exhibits two typical grasping patterns. Napier (1956) elaborated this concept, showing that the diversity of prehensile activities of the human hand could be comprehended within the framework of two basic functional modes – the power and the precision grips. Napier (1960) further showed that pongids display gripping postures which differ from those of man. These were valuable behavioural studies but were perhaps somewhat prejudiced by the prevailing dictum emphasizing the essential primitiveness of the human hand; indeed Napier (1961) held the opinion that the hand structure evidenced by living anthropoid apes was such a specialized end product that it was of little value as a model for a possible stage in human evolution.

In recent years a great body of data – anatomical, molecular, serological and karyological – has been assembled which seems virtually to clinch the hypothesis of a close phylogenetic relationship between man and the African great apes. Opinions may differ about the dating of their initial divergence, and few would deny that the chimpanzee and gorilla possess specializations of their own, such as a relatively small thumb and certain knuckle-walking characteristics, but outright disclaimers of the central thesis are in a shrinking minority.

This paper is concerned with attempting to establish morphological markers which can be associated with the unique functions of the human hand and distinguish it from those of other hominoids. Given the essential evolutionary plasticity of anatomical structures it would be remarkable if some two million years of tool use

and manufacture, coupled with selective pressures for refined manual dexterity and a change in gripping postures, had not been reflected in basic morphological changes.

Previous studies in this field have been amost exclusively concerned with the thumb and its joints. The present study details other joint changes which seem to have played an indispensable part in shaping the human hand. A preliminary attempt is then made to apply this data to certain of the hominid fossils now available.

MATERIAL AND METHODS

The following formalin-fixed wet specimens from the author's collection were utilized: *Caluromys lanatus* (woolly opossum), *Pseudochirus laniginosus* (ringtailed possum), *Tenrec ecaudatus* (tailless tenrec), *Lemur catta* (male ringtailed lemur), *Lemur fulvus* (juvenile male brown lemur), *Galago crassicaudatus* (thick-tailed bush baby), *Perodicticus potto* (Bosman's potto), *Callithrix geoffroyi* (female white-fronted marmoset), *Leontideus rosalia* (male golden lion tamarin), *Saimiri sciureus* (female squirrel monkey), *Cebus albifrons* (female white-fronted capuchin), *Aotus trivirgatus* (male douroucoli), *Lagothrix lagotricha* (Humboldt's woolly monkey), *Colobus polykomos* (black and white colobus monkey), *Procolobus verus* (olive colobus monkey), *Presbytis obscurus* (dusky leaf monkey), *Papio papio* (Guinea baboon), *Cercopithecus neglectus* (De Brazza's monkey), *Pan troglodytes* (2 year old chimpanzee), *Pan troglodytes* (young male chimpanzee), *Gorilla gorilla gorilla* (3 year old male lowland gorilla), *Pongo pygmaeus* (adult male orang-utan), *Hylobates lar* (adult male lar gibbon). In addition 14 hands from dissecting room cadavers were specially dissected. These various specimens will not be formally described in detail but will be mentioned in the text where the findings are relevant.

Osteological observations were carried out on macerated material in the author's collection and this was supplemented by the wide range of material available in the British Museum (Natural History). This material will not be formally described but again will be mentioned where appropriate; specimens from the latter source which are particularized below are identified by their catalogue numbers.

Casts of the fossils mentioned in this paper were available at the British Museum (Natural History), and these have been used for the illustrations. The originals of the hand bones attributed to '*Homo habilis*' (OH7), and found in Bed I, Olduvai Gorge, were studied at the National Museum of Kenya, Nairobi.

OBSERVATIONS AND DISCUSSION
The carpometacarpal joint of the thumb
Homo sapiens

The obvious importance of this joint in manual dexterity has provided the stimulus for a number of anatomical investigations. The results to be described here are generally in fairly good accord with past observations but the relevant osteology is described, for the most part, for the first time.

The joint surfaces are markedly concavo-convex or saddle-shaped. In an instructive analysis of the form of the joint surfaces Kuczynski (1974) has pointed out that the dorsal part of the trapezial surface, adjacent to the second metacarpal, is essentially
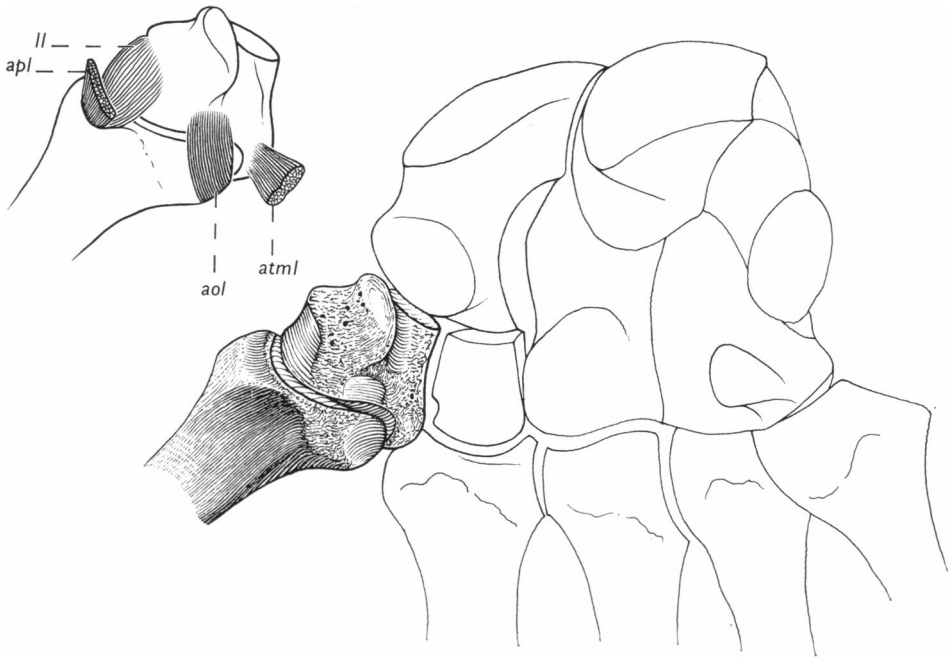
Fig. 1. A ventral view of the human carpus showing the osteological features described in the text for the trapezium and base of the first metacarpal. The inset shows the relationships of the attachments of the anterior oblique carpometacarpal ligament (*aol*), the lateral carpometacarpal ligament (*ll*), the anterior trapeziometacarpal ligament (*atml*), and the insertion of the tendon of abductor pollicis longus (*apl*), to this bony conformation.

a convex ridge; the concave element of the sellar surface is a consequence of the downward deflexion of the broad and rather flattened ventral part of the surface, creating a curved trough passing from the radial to the ulnar side. The fibrous capsule shows intrinsic ligamentous thickenings. The anterior oblique carpometacarpal ligament (Fig. 1) passes from a smooth, facet-like impression of compact bone just distal to the base of the tubercle (crest) of the trapezium to an impression on the volar tongue-like projection of the first metacarpal. The thick lateral carpometacarpal ligament passes from a second smooth impression on the lateral aspect of the trapezium to the lateral aspect of the base of the first metacarpal; this ligament is here covered by the insertion of the tendon of abductor pollicis longus, with a bursa intervening.

Dorsally (Fig. 2), the posterior oblique ligament arises from a prominent bony tubercle laterally situated on the trapezium; this dorsal tubercle is not to be confused with the tuberculum ossis trapezii (PNA) which is the crest overhanging the groove for the tendon of flexor carpi radialis. The distal aspect of this dorsal tubercle is smoothly truncated and is confluent around the lateral border of the trapezium with the impression for the lateral ligament. From this restricted bony origin the posterior ligament fans out to become inserted along the whole dorsal margin of the metacarpal base; the adjoining borders of this ligament and the lateral ligament are confluent.
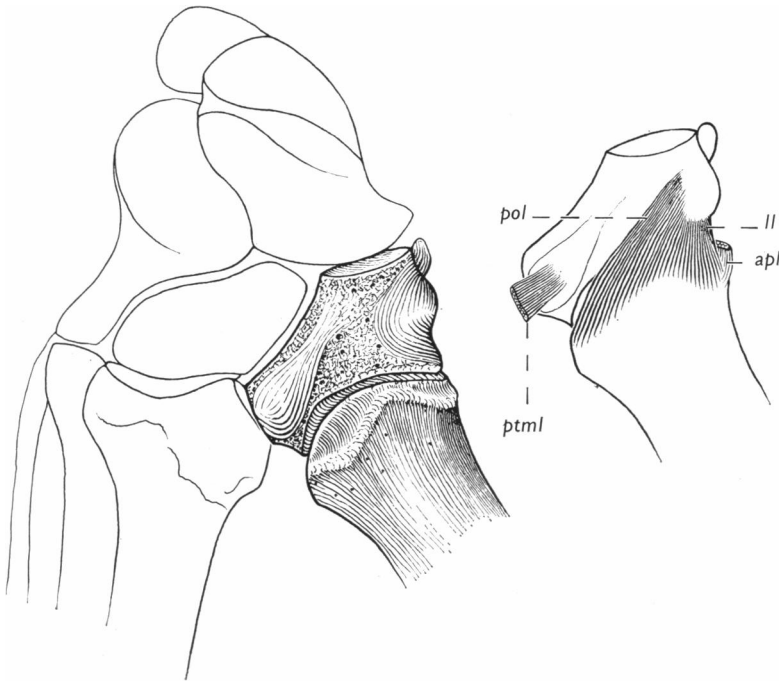
Fig. 2. A dorsal view of the human trapezium and base of the first metacarpal showing the osteological features described in the text. The inset shows the relationships of the attachments of the posterior oblique carpometacarpal ligament (*pol*), the lateral carpometacarpal ligament (*ll*), the posterior trapeziometacarpal ligament (*ptml*), and the insertion of the tendon of abductor pollicis longus (*apl*), to this bony conformation.

Fick (1904) described the ligamentous apparatus of this joint and recognized a L. trapezio-metacarpeum pollicis dorsalis, arising from a dorsoradial tubercle on the trapezium, and a L. trapezio-metacarpeum pollicis volaris. The account is confused and the illustrations bear little resemblance to the true morphology. Poirier & Charpy (1911) gave an account similar to that of Fick.

Haines (1944) recognized and described the three ligaments noted above but strangely he figured the posterior oblique ligament as radiating from a restricted origin on the metacarpal to a broad insertion on the trapezium, instead of *vice versa*; he was not concerned with the underlying osteology.

Napier (1955) gave a description in good accord with that presented above but without particularizing osteological features. Quite accurate illustrations of the ligaments have, in fact, long been available (Weitbrecht, 1742).

Pan troglodytes

The joint surfaces are saddle-shaped as in man but that on the trapezium is less broad (Figs. 35, 37), reflecting the relatively flattened form of the bone. Owing to the orientation of the trapezium within the carpal arch, the homologue of the human palmar surface of the bone faces almost directly medially (Fig. 9).

The joint possesses an anterior oblique ligament, disposed similarly to that of man,

though of flimsier texture. As in man, a strong posterior oblique ligament radiates from a prominent dorsal tubercle on the trapezium (Figs. 34, 36) to a broad attachment on the metacarpal base. No identifiable lateral ligament exists; where one might have expected it the fibrous capsule is thin and is covered by the dual insertion of the tendon of abductor pollicis longus to the trapezium and first metacarpal.

Gorilla gorilla gorilla

The joint surfaces are again saddle-shaped, that on the trapezium being broader than is usual in the chimpanzee, thus approaching more nearly the condition seen in man.

The ligamentous apparatus is similar to that of the chimpanzee. The strong posterior oblique ligament again arises from a dorsal bony tubercle, which is the site of a striking and unique specialization. Adjacent to this tubercle the trapezium has sprouted a massive bony apophysis (Figs. 38, 39), lying behind the tubercle proper (or crest) of the trapezium and mimicking it. Even more surprisingly, this process extends far enough proximally to establish a supernumary articulation with the tubercle of the scaphoid. This is the usual condition in *Gorilla gorilla gorilla* (B.M. 1951.9.27.11, and five other specimens) but in a ligamentous preparation (B.M. 1948.3.31.1) the apophysis existed as a separate ossicle; in three other macerated specimens (e.g. B.M. 1948.436) no apophysis was present, but at its usual site was a facet, strongly indicative of the previous presence of a free bony element detached during maceration. The fully formed apophysis is also found in *G. g. beringei* (B.M. 1961.4.5.1). It seems likely that the bony process is derived from the prepollex, and, on occasion, may persist as a separate bony element.

Pongo pygmaeus

The joint surfaces are typically and unequivocally saddle-shaped (B.M. 1948.10.25.1; B.M. 1948.11.23.1). In other cases the ventral overhang on the trapezium may be considerably reduced (B.M. 1948.7.6.3) and the author has in his possession a specimen in which this part of the bone is markedly swollen, thus representing an intermediate stage in a trend which, if carried somewhat further, could result in the condition seen in gibbons, where the trapezium presents a convex, ball-like articular surface. A posterior oblique ligament radiates from a dorsal tubercle on the trapezium and an anterior oblique ligament is present. No specialized lateral ligament is detectable and the capsule is, in fact, overlaid laterally by the bony prepollex receiving part of the insertion of the tendon of abductor longus pollicis.

Hylobates lar

As is well known, gibbons possess a ball and socket joint at the base of the thumb metacarpal, with the convex (male) surface being located on the trapezium. There are reasonable grounds for assuming that this is a secondary specialization and the joint surface on the first metacarpal may show suggestive indications of derivation from the sellar shape typical of other hominoids. Indeed, as noted above, some specimens of *Pongo pygmaeus* show a significant approach towards the hylobatid form.

As in the pongids described, an anterior oblique ligament is present and a strong posterior oblique ligament radiates from a bony dorsal tubercle on the trapezium.

The phylogenetic background

Even in marsupials (*Pseudochirus laniginosus* and *Caluromys lanatus*) the joint surfaces are concavo-convex and foreshadow the refined sellar form found in higher primates. Thus, dorsally the trapezial surface is essentially cylindrical but the ventral margin is hooded over, impressing a concave element on the overall form; the fundamentals of the articular surface of *Homo sapiens* (Kuczynski, 1974) are then detectable even in marsupials. The fibrous capsule even shows ligamentous thickenings, which may be designated anterior and posterior ligaments (Fig. 10) because of their apparent homology with similar structures found in the primates (and man); these terms are not always descriptively apt because of variations in the orientation of the trapezium. The former ligament is quite slender, and the latter is a broad sheet which is not concentrated on to a bony tubercular origin on the trapezium and not therefore oblique and fan-shaped.

In quite generalized insectivores (*Tenrec ecaudatus*) a similar arrangement obtains, and this may also be observed in prosimians (*Perodicticus potto*, *Galago crassicaudatus*). Haines (1958) has further demonstrated that the metacarpal surface of the trapezium is saddle-shaped in the carnivore *Herpestes ichneumon* and in the tree-shrew *Ptilocercus lowii* and has suggested that some degree of opposability of the pollex is more common in mammals than is generally admitted, despite its usually very limited degree of independence and divarication from the other digits. Jouffroy & Lessertisseur (1959) have also commented upon the saddle-shaped form of the joint in lemuroids.

In New World monkeys definite indications of the presumably primitive concavo-convex form, with similar anterior and posterior ligaments, may also be quite obvious (*Aotus trivirgatus*, *Lagothrix lagotricha*, *Cebus albifrons*, *Saimiri sciureus*), although there is a tendency towards some degree of suppression of the ventral concave element of the trapezial surface; indeed, in this *Cebus albifrons* is not unlike *Pongo pygmaeus*. In the Callitrichidae (*Callithrix geoffroyi*, *Leontideus rosalia*), however, the concave element of the trapezium surface is even further suppressed, leaving the joint surface largely cylindrical. In Old World monkeys (*Colobus polykomos*, *Procolobus verus*, *Cercopithecus neglectus*, *Papio papio*) the joint surfaces are usually unequivocally concavo-convex with anterior and posterior ligaments, the latter again being a flat sheet. In *Presbytis obscurus*, however, the concave element of the trapezial surface is diminished, paralleling the form observed in *Cebus albifrons*.

The joint surfaces, thus, have not undergone any particularly dramatic change during evolution. The notion (Napier, 1961), therefore, that a sudden change in direction of evolution produced a saddle joint which has been evolved only in Old World monkeys, apes and man, leaving other generalized mammals with a mere hinge joint (and a 'modified hinge' in New World monkeys) is misleading. Whilst detailed consideration of the complex joint surfaces in mammals other than the hominoids is beyond the scope of this paper, it is clear that the essence of the concavo-convex form is an ancient mammalian attribute, although in diverse groups some rounding off of the ventral concave element of the trapezial surface has occurred resulting in an almost cylindrical, or even spherical, shape. In the Hominoidea alone, however, has the posterior ligament become truly oblique and fan-shaped, with a carpal origin concentrated on to a bony tubercle on the trapezium. Broadening of the

lateral surface of the trapezium in man has apparently been accompanied by the partial sequestration of a part of this ligament to form the lateral ligament. The osteological correlates of the hominoid ligamentous apparatus are not as precise as one might wish. In New World monkeys the lateral surface of the trapezium bears a columnar apophysis which might be confused with a dorsal tubercle for ligamentous attachment. This projection (which recalls a similarly located outgrowth in *Gorilla*) is, in fact, for articulation with the bony prepollex which is lodged between it and the scaphoid tubercle; these features can be clearly identified in ligamentous preparations (*Cebus apella*, B.M. 1948.10.20.1 and B.M. 3.9.1.4; *Aotus trivirgatus*, B.M. 1863.11.90.1 and B.M. 3.9.1.8). A similarly located, but stunted, bony prominence may be found in Old World monkeys. It is especially prominent in baboons, where it again serves for articulation with a bony prepollex (*Papio cynocephalus*, B.M. 1961.8.9.3); in other cercopithecoids it may be barely perceptible. This elevation does not appear to be homologous with the dorsal tubercle of hominoids and is indeed rather different in appearance and situation. It is of interest that the Miocene ape *Dryopithecus* (*Proconsul*) *africanus* possessed a dorsal tubercle of apparent hominoid type (Fig. 43), indicative of the acquisition at this stage of the hominoid ligamentous apparatus. The metacarpal joint surface of the trapezium also shows the usual concavo-convex features; the contention (Napier, 1964) that this fossil lacked a sellar joint cannot be substantiated.

The metacarpophalangeal joints

Pan troglodytes

The heads of the metacarpals (Fig. 3) (except the first) in this knuckle-walking ape possess, as is well known, dorsal ridges which act as articular stops for the proximal phalanx in hyperextension. These, however, are variable in development and may be virtually non-existent (B.M. 1882.9.18.1), especially in young animals. For the remainder of this account they will be largely disregarded, since there is no good evidence that such specializations occurred at any stage in human evolution. The remainder of the metacarpal heads form relatively uncomplicated ellipsoidal surfaces. The distal articular surface is formed not only by the phalangeal base but also by the thick palmar ligaments. As in man these structures are deeply grooved ventrally for the flexor tendons, and are flexibly hinged at the phalangeal bases; in the French anatomical literature the human homologues are known as 'glenoid fibrocartilages or plates'. In the immature specimens dissected no metacarpophalangeal sesamoid bones were found and in an adult ligamentous preparation (B.M. 1948.8.6.1) the only sesamoid present is a radial one at the joint of the thumb. Retterer & Neuville (1918) similarly noted the absence of sesamoid bones in the chimpanzee. The joint is flanked on either side by collateral ligaments having an eccentric origin from the region of the lateral tubercles on the metacarpal heads and inserting on to both phalanx and glenoid plate. Effectively, the structure and function of the joints are comparable to the situation usually held to obtain in the human joints (e.g. Kapandji, 1966): the joints have two degrees of freedom of which flexion–extension is the major one and is essentially a hinge motion; some degree of abduction–adduction is also permitted in extension. The heads of the second and fifth metacarpals show some asymmetry, that of the index being slightly bevelled off dorsoradially whilst that of the minimus gives the impression of having been pared
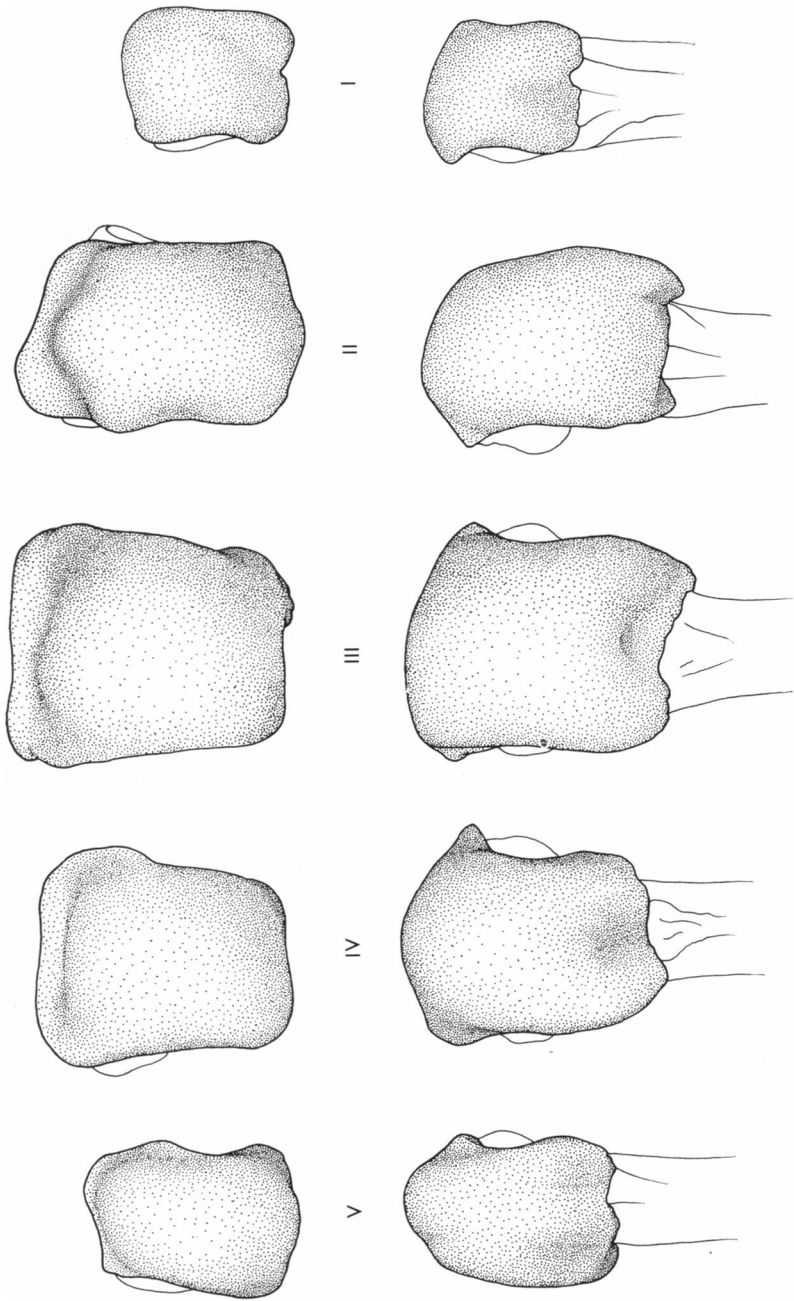
O. J. LEWIS

Fig. 3. The metacarpal heads (numbered) from the right hand of *Pan troglodytes* (B.M. 1948.10.25.2) viewed from directly distally (above), and from an angle of 45° distoventrally (below).

away on the dorso-ulnar aspect. These same metacarpals show slight grooving ventrally on the heads where the margins of the glenoid plates engage, these grooves partially delimiting small marginal elevations. Well developed knuckle-walking ridges obscure the bevelling and the asymmetry is more obvious when these ridges are poorly developed. The resultant asymmetrical form of the metacarpal heads modifies movement somewhat; extension of the index joint is accompanied by some ulnar deviation of the digit, this being facilitated by relaxation of the radial collateral ligament over the bevelled off part of the head; the converse movement occurs in the minimus.

The head of the thumb metacarpal is slightly bevelled off dorsally on the radial side and volarly presents a radial elevation, whose functional import will be discussed later.

Gorilla gorilla gorilla

The morphology agrees in all essentials with that of the chimpanzee.

Pongo pygmaeus

No knuckle-walking ridges are, of course, found on the metacarpals of the orang-utan. The form of the metacarpal heads is quite comparable to those immature specimens of *Pan* or *Gorilla* in which knuckle-walking ridges are virtually non-existent. Again, the head of the metacarpal of the index finger shows dorsoradial bevelling, and that of the minimus shows dorso-ulnar bevelling; the functional implications of this asymmetry are as for *Pan*. The head of the thumb metacarpal is also dorsoradially bevelled and presents a radial elevation volarly.

Hylobates lar

The heads of the metacarpals in this species have a conformation more in keeping with simple hinge joints. Asymmetry is scarcely detectable on the index metacarpal but more apparent on that of the minimus. The thumb metacarpal, as in the previous species, shows some asymmetry and a radial elevation volarly.

The phylogenetic background

Consideration of the primeval mammalian pattern does much to elucidate the history of these joints among the primates. The distal articular surfaces of the basic mammalian joints are, of course, formed in part by the concave bases of the proximal phalanges, but hinged on to the ventral margins of these are the thick fibrocartilaginous glenoid plates, which form an integral and perhaps even more important part of the distal (female) articular surface. The volar surfaces of the glenoid plates are deeply grooved for the long flexor tendons and form channeled guides directing the trajectory of the long flexor tendons at their entrance to the fibrous flexor sheaths of the digits. The thickened lateral margins of the glenoid plates are typically reinforced by ossifications, the so-called digital sesamoids. These ossific nodules are analogous to lunulae, shown by Barnett (1954) to be similar strengthening modifications in the thickest parts of intra-articular fibrocartilaginous menisci. A similar notion of the role of sesamoids as guides for the long flexor tendons has been voiced, at least for interphalangeal sesamoids, by Wirtschafter & Tsujimura (1961), who likened their function to that of the grooved bridge of a violin, directing and controlling the course of the strings.

These digital sesamoids are a source of considerable confusion. It is commonly stated, at least in British textbooks (e.g. Jones, 1949), that these ossicles are located within the tendons of insertion of intrinsic hand muscles and are thus comparable to other intratendinous sesamoids. It is difficult to see how this notion could be reconciled with the occasional occurrence of sesamoids at the interphalangeal joints. In contrast, French anatomists (Testut, 1904) distinguish between 'sésamoïdes periarticulaires' and 'sésamoïdes intra-tendineux', the metacarpophalangeal sesamoids being of the former type. It is, however, true that, phylogenetically, certain of the intrinsic muscles may secondarily become attached to the surface of these sesamoids (Lewis, 1965), as for example in the case of the human thenar muscles.

The glenoid plates seem to play almost a lead role in movement at the metacarpophalangeal joints. As the digit is flexed the glenoid plate moves up over the metacarpal head in a sled-like fashion, trailing the phalanx in its wake. The thick lateral margins, with their embedded sesamoids, act as runners and travel in deep grooves in the metacarpal head, which thus presents a typically fluted appearance. Between the grooves is a prominent volar crest or beak. The grooves are flanked by raised margins which are prolonged proximally as small tongue-like extensions of the volar surface. The articular surfaces of these rims extend on to the lateral surfaces of the head as flat cartilage-clothed areas against which the collateral ligaments rub during flexion.

Motion at these joints is fundamentally a hinge action, with some abduction–adduction permitted in extension. The heads of the second and fifth metacarpals are typically asymmetrical dorsally, that of the index being somewhat bevelled off on the radial side and that of the minimus on the ulnar side. Thus as the index digit moves into extension it deviates to the ulnar side (owing to its passage over the twisted metacarpal head, and slackening of the radial collateral ligament over the bevelled-off part of the metacarpal head); this is associated with conjunct rotation in the sense of supination (exorotation). Movements in the minimus are the converse of these. It is suggested that the functional import of this modified movement in the marginal digits is as follows: the digits in these quadrupedal animals will thus be aligned together, with the rotation causing their volar surfaces to be flatly applied to the substrate, cancelling out the effect of the transversely arched form of the palm. The head of the first metacarpal typically shows asymmetry similar to that of the index, with a bulbous enlargement of the radial part of its volar surface.

This basic mammalian arrangement is seen in, for example, the marsupial *Caluromys lanatus* and the insectivore *Tenrec ecaudatus*. In *Perodicticus potto* and *Galago crassicaudatus* the fluting of the metacarpal heads is largely suppressed, despite the presence of sesamoids. In the latter species the second and fifth metacarpals show typical asymmetry, but in the former species, not surprisingly, the head of the metacarpal of the rudimentary index finger shows no asymmetry, although that of the minimus does.

In Old World monkeys (*Procolobus verus, Papio cynocephalus*, B.M. 1948.3.30.1 and B.M. 1962.7.6.13) the essence of the primitive arrangement is retained with deeply grooved and crested metacarpal heads, dorsoradial bevelling of that of the index, and apparent paring away of the head on the dorso-ulnar side of the fifth metacarpal.

In New World monkeys (*Lagothrix lagotricha, Cebus albifrons*), in contrast, the fluting of the metacarpal heads is largely suppressed, despite the presence of sesamoids, as is the asymmetry of the metacarpal heads of the index and minimus. The thumb metacarpal, however, shows obvious dorsoradial bevelling and the radial margin of the lateral sesamoid groove is swollen into a cam-like formation, which by tightening the over-riding collateral ligament during flexion imparts an element of abduction and endorotation to the phalanx. As noted above, this is foreshadowed in more primitive mammals. This would seem to be the biomechanical basis of what Napier (1961) called pseudo-opposability. It is to be noted, however, that this author misinterpreted the mechanics of the joint by considering that the asymmetry of the head promoted abduction and endorotation in extension.

Homo sapiens

Textbook accounts invariably dismiss the human metacarpophalangeal joints as simple ellipsoidal joints with two degrees of freedom. Following Fick (1911) it is usually added that radial and ulnar deviation are restricted in flexion because of the obliquity of the collateral ligaments, which pass from their dorsal attachments at the lateral tubercles (and depressions in front of these) to divergent attachments to the phalangeal base and glenoid plate.

Landsmeer (1955) further refined these functional ideas by introducing the notion that rotation plays a significant part in normal movements. He suggested that ulnar deviation* ('ulnar abduction') is freer than radial deviation and that the former movement is accompanied by supination (exorotation) of the finger and the latter by pronation (endorotation). He attributed this differential freedom to the contrasting obliquity of the radial and ulnar collateral ligaments: the radial ligaments being more oblique (or in the case of annularis and minimus, having a more distal metacarpal attachment) are rendered more lax by rotation than are those on the ulnar side.

The heads of human metacarpals, particularly the second and fifth (Figs. 4, 5), are asymmetrical. Strangely, Landsmeer (1955) ignored the fact that the fifth is virtually a mirror-image of the second; clearly, this is not in accord with his concept of freer ulnar deviation in all digits. His accurate anatomical study usefully focused attention on rotation in these joints; it appears, however, that this plays a wider role than that of a mere ancillary factor increasing deviation.

The distal (female) articular surface of each joint consists not only of the oval, concave area on the phalangeal base but also of an integral and functionally important palmar ligament, the fibro-cartilaginous glenoid plate (Fig. 6). This glenoid plate is flexibly hinged to the phalangeal base and only loosely attached proximally to the metacarpal where there is a ballooning synovial pouch (McMaster, 1972).

The proximal (male) articular surface shows considerable differences in the various digits (Figs. 4, 5). At one extreme is the index metacarpal; here the articular surface consists of a central segment which is convex and follows a spiral course dorsally, deviating to the ulnar side so that the head is effectively bevelled off dorsally and radially. Confluent with either side of the volar end of this segment, but delimited by

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* These terms are preferable to 'radial and ulnar abduction' as used by Landsmeer (1955), since abduction and adduction of the fingers are usually considered as movements in relationship to a hand axis formed by the middle digit.
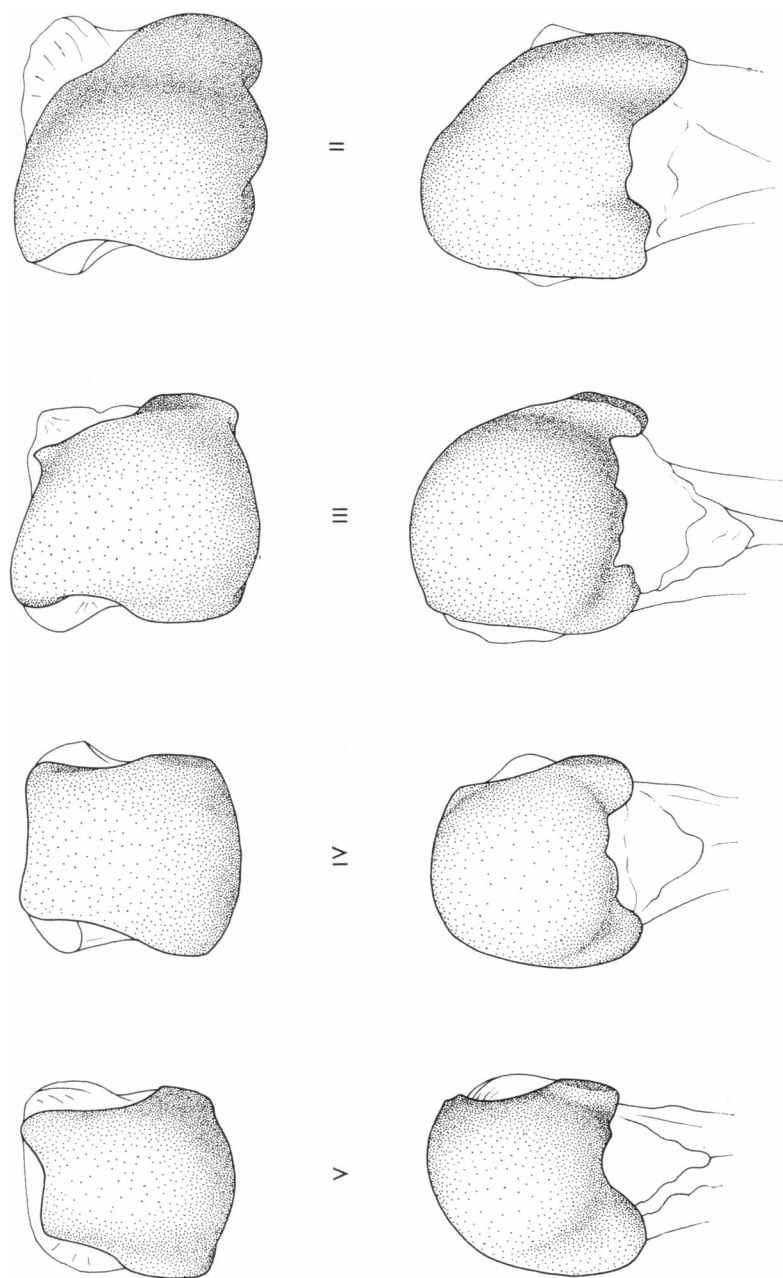
Fig. 4. The heads of the metacarpals of the index (II), medius (III), annularis (IV) and minimus (V) of the right hand of *Homo sapiens*, all viewed from standardized positions: above, from directly distally; below, from an angle of 45° distoventrally (the flattened distal part of the dorsal surface of the shaft being used as a plane of reference).
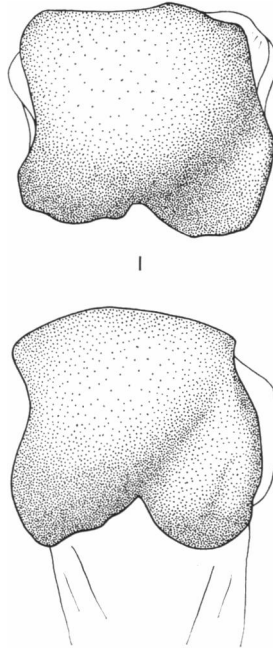
Fig. 5. The head of the metacarpal of the thumb (I) from the right hand of *Homo sapiens* viewed from distally (above) and from an angle of 45° distoventrally (below).

shallow grooves, are two additional articular components – a small convexity at the ulnar side and a large bulbous protuberance radially.

When the phalanx is extended (Figs. 6A, 7A) it automatically deviates to the ulnar side on the twisted metacarpal head and becomes exorotated (supinated), the form of the articular surface naturally guiding it into this position, whose attainment is facilitated by the dorsolateral excavation of the head which affords free passage, and ensuing laxity, to the radial collateral ligament. The glenoid plate takes up its position on the distal and volar part of the central area of the articular surface. This ulnar deviation of the phalanx determines that the groove for the flexor tendons in the glenoid plate becomes so orientated that the tendons must enter the fibrous flexor sheaths of the digit along a markedly angled pathway.

When the finger moves into full flexion (Figs. 6B, 7B) the following sequence of events occurs. The base of the phalanx rides up the spiral central articular area, preceded by the glenoid plate which finally considerably over-rides the proximal margin of the articular surface, being facilitated in this by the laxity here of its capsular attachment (Gad, 1967; McMaster, 1972). The thickened margins of the glenoid plate, perhaps reinforced by ossific nodules (the digital sesamoids), ride into the grooves at the posterolateral corners of the central area. As this motion progresses the broad radial collateral ligament becomes progressively tensed over the swollen lateral articular cam-like projection. This has the effect of rotating the phalanx in the sense of pronation (endorotation) and of pulling it from an attitude of ulnar deviation towards radial deviation. The ulnar collateral ligament is similarly
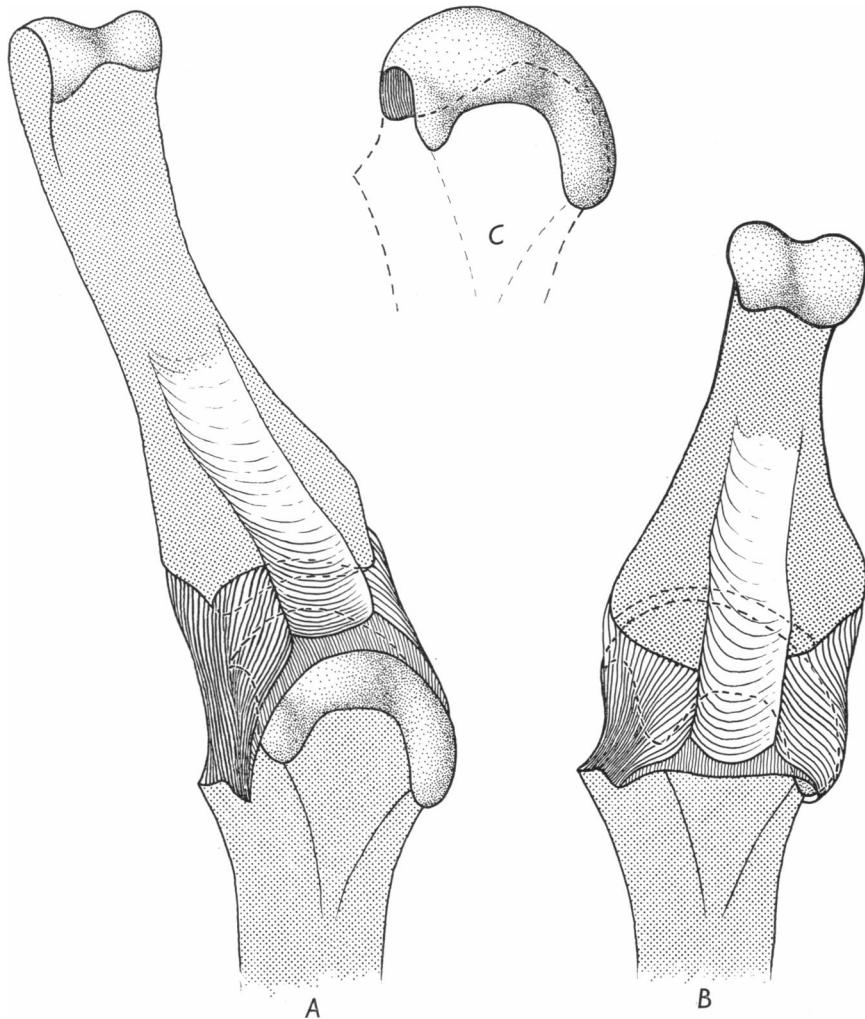
Fig. 6. A diagram illustrating the mechanics of the movements at the metacarpophalangeal joint of the right index finger of *Homo sapiens* reconstructed from radiographs of a ligamentous preparation in which salient features – the articular margin of the metacarpal head and the flexor groove in the glenoid plate – were outlined with metal markers. *A*, the joint in full extension; *B*, in full flexion; *C*, the form of the 'isolated' articular surface of the metacarpal head.

stretched over the comparatively small medial articular cam. The entry of the long flexor tendons into the fibrous sheath is no longer angulated; having entered the palm from the carpal tunnel they pursue a straight course into the fibrous flexor sheath of the finger. In executing this movement the mechanical axis of the proximal phalanx has described an arcuate course over the metacarpal head and this is associated with conjunct rotation, as one would expect from the basic principles of joint mechanics enunciated by MacConaill (1953) and MacConaill & Basmajian (1969).

In the same hand, the head of the fifth metacarpal (Fig. 4) has a form which is the
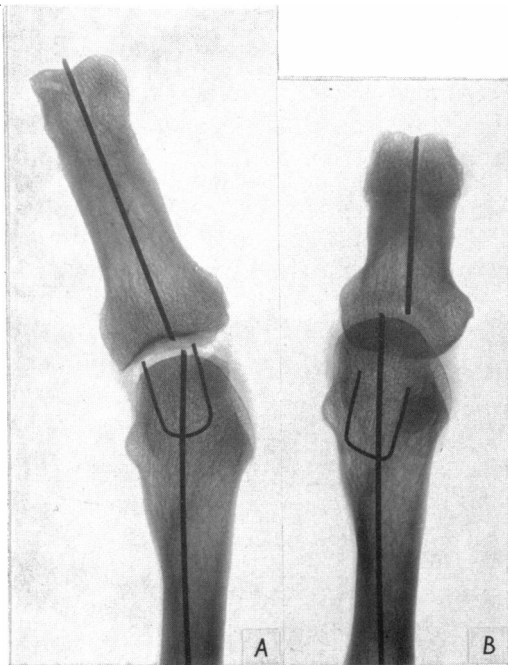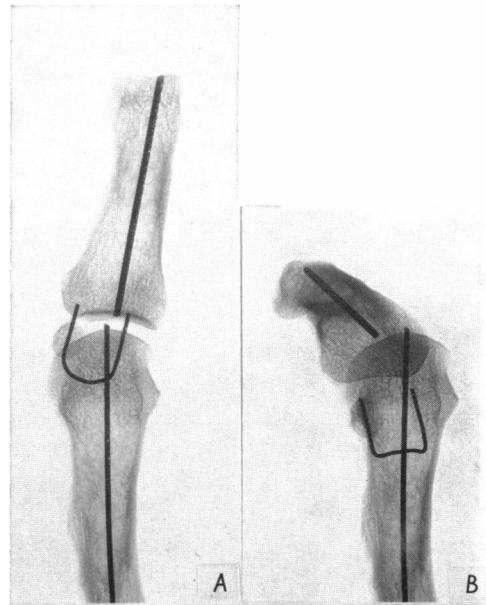
Fig. 7   Fig. 8

Figs. 7*A* and 7*B*. Radiographs of a ligamentous preparation of the metacarpophalangeal joint of the right index finger of *Homo sapiens* with the movements highlighted by metal markers inserted along the mechanical axes of the second metacarpal and proximal phalanx and outlining the margins and proximal limit of the flexor groove in the glenoid plate (which contains a radial sesamoid). *A*, in full extension; *B*, in full flexion.

Figs. 8*A* and 8*B*. Radiographs of a ligamentous preparation of the metacarpophalangeal joint of the right minimus of *Homo sapiens* with metal markers inserted along the mechanical axes of the fifth metacarpal and proximal phalanx and outlining the margins and proximal limit of the flexor groove in the glenoid plate (which contains an ulnar sesamoid). A, in full extension; B, in full flexion.

mirror-image of the index metacarpal. In all essentials the movements are the opposite of those occurring in the index: at full extension (Fig. 8A) the phalanx is in a neutral position, or slightly radially deviated, and pronated; in moving into full flexion (Fig. 8B) it becomes supinated and abducted.

The joint of the ring finger lacks the asymmetrical type of metacarpal head found in the index and minimus and flexion and extension are practically simple hinge movements as in the chimpanzee. In the middle finger the metacarpal head shows a minor degree of modelling comparable to that of the index, and clearly flexion–extension movements are accompanied by lesser degrees of rotation and deviation.

The metacarpophalangeal joint of the thumb shows considerable plasticity of form, and in at least 10 % of cases the metacarpal head is quite flat distally (Joseph, 1951). Typically, however, (Fig. 5) the metacarpal head shows some dorsoradial bevelling. The articular surface shows two volar prolongations, a flattened area medially and a convex cam laterally for articulation with the suitably shaped deep

surfaces of the radial and ulnar sesamoids, designated rather aptly by Testut (1904) as 'scaphoïde du pouce' and 'pisiforme du pouce' respectively. It is clear that some degree of endorotation and abduction accompany flexion, as occurs in the index finger. This then is the biomechanical basis for the contribution made by the metacarpophalangeal joint to opposition of the thumb, noted by Napier (1956). As mentioned above, this articular arrangement is apparently an ancient mammalian attribute.

The second to fifth carpometacarpal joints

With the notable exception of man, all hominoids present a fundamental morphological pattern in these joints which is basically similar in its essentials and is clearly a pattern of common inheritance. Indeed, this same pattern can be found throughout the Anthropoidea.

Pan troglodytes

The third metacarpal firmly abuts on the capitate and is braced on either side by interosseous carpometacarpal ligaments (Fig. 9, upper); anterior and posterior to these ligaments the bases of the second and fourth metacarpals articulate with the third, the adjoining sides of these metacarpal bases thereby possessing dual facets. The second metacarpal is stabilized by deep indentation into the carpus, articulating medially with the side of the capitate by proximal extensions of the dual intermetacarpal facets. The second metacarpal also bears a facet on the posterolateral aspect of its base (just anterior to the impression where the tendon of extensor carpi radialis longus is inserted) for the trapezium. A strong ligament radiates towards the palm from the trapezium in front of this articulation and attaches to the second and third metacarpals; a similar ligament joins the trapezium posteriorly to the second metacarpal. Both the fourth and fifth metacarpals articulate with the distal aspect of the hamate, which here presents dual convex facets ballooning distally and articulating with concavities in the metacarpal bases, which additionally have a single intermetacarpal joint between them. The fourth metacarpal extends beyond the hamate posteriorly to achieve a small contact with the capitate. In striking contrast to man the hook of the hamate overhangs the bases of the fourth and fifth metacarpals and articulates with them. The facets on the metacarpals for the hamate hook are convex, and are sharply angled to those concave ones on the proximal aspects of their bases for the body of the hamate (Figs. 9, upper, and 22). A massive pisohamate ligament anchors the pisiform to the hook of the hamate and some of its substance continues on medially to the base of the fifth metacarpal as the pisometacarpal ligament.

Gorilla gorilla gorilla

The whole pattern of articulation is similar to that of Pan. The ligamentous apparatus is also identical, with all the same clearly definable bands: interosseous carpometacarpal ligaments flanking either side of the third metacarpal; an anterior trapeziometacarpal ligament (attaching to the second and third metacarpals) and a posterior trapeziometacarpal ligament (passing to the second metacarpal); a pisometacarpal ligament passing to the fifth metacarpal.
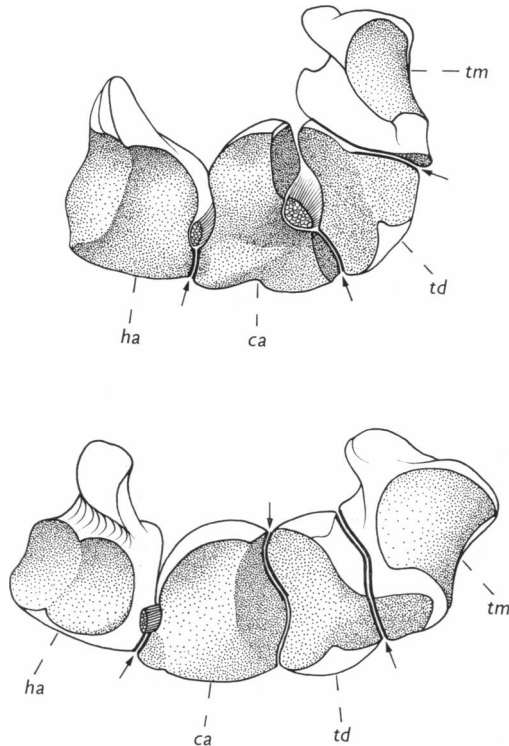
Fig. 9. Above, the distal aspect of the left carpus of a wet specimen of *Pan troglodytes* (the same specimen as is shown in Fig. 13). Below, the distal aspect of the left carpus of a wet specimen of *Homo sapiens*. In each case the bones are figured with the midcarpal joint in full extension. Articular surfaces are shown in heavy line and are indicated by arrows. *tm*, trapezium; *td*, trapezoid; *ca*, capitate; *ha*, hamate.

Pongo pygmaeus

Again the same articular and ligamentous pattern is found.

Hylobates lar

The pattern is again similar, but showed a minor modification in the wet specimen dissected, perhaps of minor interest in itself but significant for the way in which it demonstrates the sort of evolutionary trends which may affect these joints. The interosseous carpometacarpal ligament passing from the capitate between the third and fourth metacarpals was a rudimentary flattened band whose regression had permitted the confluence of the anterior and posterior facets on each of the adjacent metacarpals.

The evolutionary background

Old World monkeys (*Colobus polykomos*, *Papio papio*) present a quite similar articular pattern to that of the pongids described. It was noted for *Hylobates lar* how regression of the interosseous carpometacarpal ligament on the ulnar side of the third metacarpal can permit confluence of the anterior and posterior facets between this

bone and the fourth metacarpal. In the dissected specimen of *Papio papio* an ana-
logous process had occurred on the opposite (the radial) side of the third metacarpal.
Here the carpometacarpal ligament was represented only by a slender thread,
allowing confluence of the articular facets in front and behind it on both capitate and
index metacarpal. This is of particular interest since it is a specialization convergently
foreshadowing a human specialization.

There is ample indication also that the basic articular pattern in New World
monkeys was also similar to that persisting in the pongids, modified, however, in
certain species by regression of one or other of the carpometacarpal ligaments
flanking the base of the third metacarpal. Only that on the radial side is present in
the marmoset *Callithrix geoffroyi*; in the tamarin *Leontideus rosalia* only that on the
ulnar side is found. The latter condition, where the radial of these two carpometa-
carpal ligaments is suppressed is, in fact, common in New World monkeys and
represents a more advanced parallel to the incipient trend noted for *Papio papio*.
Thus, in *Aotus trivirgatus*, *Lagothrix lagotricha*, *Cebus albifrons* and *Saimiri sciureus*
a virtually human condition is attained: the second metacarpal articulates by a long
linear anteroposterior facet with the capitate, no intervening carpometacarpal liga-
ment being present, and consequently no separation of this articulation into anterior
and posterior parts. The functional parallels between this and the similar arrange-
ment in *Homo sapiens* will be considered later. In *Aotus* and *Lagothrix* the ulnar
carpometacarpal ligament was also lacking. There thus seem ample grounds for
believing that the basal articular and ligamentous pattern in both platyrrhine and
catarrhine monkeys was similar to that now found in pongids. There seems to be
a clear pattern of common inheritance, albeit with easily interpretable modifications
in certain species, characterizing all the higher primates.

The essence of this pattern appears also to have represented the basic prosimian
arrangement, but with one significant difference: the ulnar side of the third meta-
carpal is slightly indented into the carpus and articulates with the hamate (in contrast
to the higher primate arrangement where the fourth metacarpal achieves a small
posterior contact with the capitate). In *Lemur fulvus* and *Lemur catta* interosseous
carpometacarpal ligaments flank either side of the capitate and third metacarpal
but despite this the facets on the second metacarpal for the capitate are confluent (cf.
Papio papio). In *Galago crassicaudatus* only the ulnar carpometacarpal ligament is
found and in *Perodicticus potto* both these carpometacarpal ligaments are lacking.
Their presence in *Lemur* supports the idea that carpometacarpal ligaments running
from either side of the capitate represent the ancestral primate condition. The
remaining elements of the ligamentous and articular pattern are similar to those in
the Anthropoidea.

In the insectivore *Tenrec ecaudatus* many of the fundamentals of the pattern
described for the Anthropoidea are present, but, as in prosimians, the ulnar side of
the third metacarpal is obtrusively indented into the carpus and articulates with the
hamate. The articulation between third and fourth metacarpals is, however, dual
with a thin and rudimentary interosseous carpometacarpal ligament proceeding
distally from the capitate. The index metacarpal has a single linear articulation with
the capitate. In all other respects the ligaments and joints follow the basal primate
arrangement. The trapezium articulates with the index metacarpal and this joint is
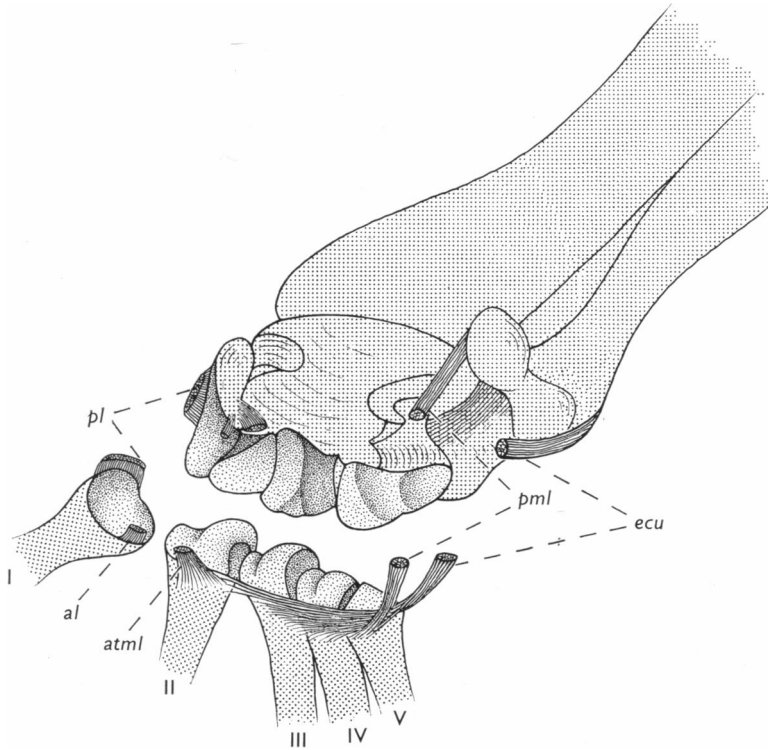
Fig. 10. The right hand of *Pseudochirus laniginosus*, viewed from ventrally, with the metacarpals (I–V) disarticulated from the carpus and displaced dorsally. *al*, anterior ligament of the first carpometacarpal joint; *pl*, posterior ligament of the first carpometacarpal joint; *atml*, anterior trapeziometacarpal ligament; *pml*, pisometacarpal ligament; *ecu*, tendon of extensor carpi ulnaris.

provided with a very strong anterior ligament, and a posterior ligament. The hamate overhangs the bases of metacarpals 4 and 5, articulating with them; this volar extension of the hamate is the clear homologue of the hook-like process typifying the Hominoidea, although in mammals other than this primate superfamily the process is usually an integral part of the body of the hamate. A pisometacarpal ligament flanks the articulation.

It is likely that something very like this was the basal therian arrangement, as is suggested by the morphology in the marsupials *Caluromys lanatus* and *Pseudochirus laniginosus*. All the features described for the tenrec are repeated here, although without even a residual carpometacarpal ligament where the third metacarpal intrudes into the carpus and contacts the hamate. Both of these marsupials, however, show a striking specialization which turns out to be convergent to a modification found in the human hand, and by analogy elucidates this latter. The extensor carpi ulnaris tendon has extended from its primitive attachment to the fifth metacarpal and traverses the palm across the bases of the metacarpals reaching as far as the second (Fig. 10). In taking this course it runs in a groove on the distal aspect of the hook of

the hamate, thus separating the bases of the fourth and fifth metacarpals from the encroachment of the overhanging hamate; indeed it here forms a labrum-like structure across the bases of the metacarpals. The arrangement strikingly mimics the course of the peroneus longus tendon in the mammalian foot. Clearly this morphology has enhanced the mobility of the postaxial metacarpals. The base of the second metacarpal has a long convex articulation with the capitate and is free of any interosseous carpometacarpal ligament convergently resembling the similar specialization found in man. Mobility of the second metacarpal is thus presumably enhanced. These specializations can be functionally correlated with the grasping mode – schizodactyly or zygodactyly – utilized by these creatures (Cartmill, 1974) in which the mobile second digit acts together with the thumb as one arm of a pincer, the other arm, also quite mobile, being formed by digits 3–5.

There are thus good grounds for believing that the essence of the morphology found in the primates today is as old as the mammals themselves and that in the higher primates (the Anthropoidea) the primitive articulation of the third metacarpal with the hamate has been suppressed and replaced by a small posterior articulation of the fourth metacarpal with the capitate. Interestingly, however, the more primitive mammalian condition persists in prosimians. It seems likely also that an interosseous carpometacarpal ligament on the radial side of the capitate represents the primitive therian condition. The material available, however, does not allow one to state this with full conviction, but at least this arrangement appears to be a primitive primate character.

Homo sapiens

Striking modifications of these morphological arrangements are present in the human hand and these are clearly of considerable significance in the evolution of human hand function.

The modifications at the base of the second metacarpal bone have been discussed in some detail by Lewis (1973) and will only be summarized here.

The articulation of the index metacarpal with the trapezoid has become saddle-shaped, rather than wedge-shaped as in other hominids (Fig. 9, lower). The interosseous ligament between the second and third metacarpals is lacking and the dual facets on the second metacarpal have been re-fashioned into a convex articular surface for the capitate and second metacarpal. It could be inferred that this change permits a small degree of flexion into the palm coupled with conjunct rotation, in the sense of pronation. This would presumably enhance the effectiveness of the similar movements described above which occur during flexion at the metacarpophalangeal joint. Although the metacarpals do seem to lack any capacity for intrinsic rotation with the hand held flat (Landsmeer & Ansingh, 1957), there are radiological indications (Van Dam, 1934) that in the clenched hand the index metacarpal is in fact pronated (and that of the minimus supinated). Comparative analogies support the interpretation that loss of the interosseous carpometacarpal ligament proceeding from the radial side of the capitate, and re-fashioning of the articulation between that bone and the index metacarpal are associated with increased mobility of that metacarpal. An incipient development of this specialization has been noted in *Papio papio*, and, significantly, baboons are noted for their quite high degree of independent
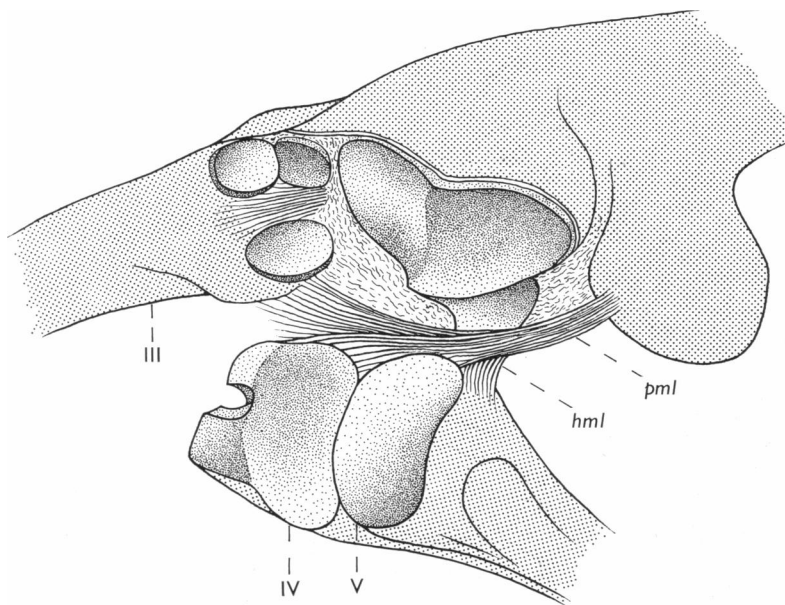
Fig. 11. The ulnar part of the carpometacarpal joint of a left hand of *Homo sapiens* opened from dorsally. The fifth metacarpal (V) is displaced ventrally from its articulation with the hamate; the fourth metacarpal (IV) is similarly displaced from its articulations with the hamate, a small adjoining facet on the capitate and dual facets (separated by an interosseous carpometacarpal ligament) on the third metacarpal (III). The pisometacarpal ligament(*pml*), clothed on its palmar surface by the hamate-metacarpal ligament (*hml*), forms the ventral wall of the joint and is displaced from its synovial-lined groove on the hook of the hamate.

control of the index finger in association with a precision grip (Bishop, 1964). Further, in mammals practising a schizodactylous, or zygodactylous, grip requiring considerable mobility of the index finger, which moves in concert with the thumb, a virtually human condition is attained. This is seen in the marsupial *Pseudochirus laniginosus* (Fig. 10) which is known to grip thus (Pocock, 1921) and in the New World monkeys *Lagothrix lagotricha* and *Aotus trivirgatus* which also practise this gripping posture (Pocock, 1925; Erikson, 1963). Examination of dry bones (Singh, 1959) shows, in rare cases, the existence of dual facets on the ulnar side of human index metacarpals, indicating the presence of a carpometacarpal ligament, and recalling the ape condition.

Further remarkable differences from ape morphology are shown in the articulations between the hamate and fourth and fifth metacarpals where the direction of curvature of the main joint surfaces is reversed: the convexity on the hamate for the fourth metacarpal is replaced by a dorsoventral concavity (Fig. 9, lower), although there is variation, and the hamate sometimes retains its convex surface (as in Fig. 11); while the facet on the hamate for the fifth metacarpal is markedly concave dorsoventrally but retains a lateral convexity – it is a sellar (saddle) surface. A much more significant change, however, has involved the hook of the hamate, which has become retracted from its enveloping grasp on the metacarpal bases. Opening the

joint from the dorsal aspect reveals the consequences of this separation (Fig. 11). A ligamentous band, part of the pisometacarpal ligament, has evolved, arching across the distal aspect of the hook of the hamate and effectively excluding it from the joint as it passes to attach to the volar surfaces of the bases of the fifth, fourth and third metacarpals, where it forms a labrum-like projection along their articular margins. It frequently directly forms the ventral wall of the joints, and the groove on the hamate hook which lodges it may be synovial lined, although in other cases a thin capsular layer separates it from the interior of the joint. The pisometacarpal ligament is invariably inaccurately described (at least in English language textbooks) as passing from the pisiform to the base of the fifth metacarpal, and the reason for this misunderstanding is not difficult to appreciate. When viewed from ventrally the arched course of the ligament is obscured by a fibrous band passing from the hook of the hamate to the fifth metacarpal. This was named the 'Haken-Mittelhandband' by Fick (1904) but, in fact, appears to be no more than the deepest, fibrosed fibres of that part of opponens minimi digiti deep to the deep branch of the ulnar nerve, described by St John Brooks (1886); indeed, it may replace that muscle bundle. A further source of confusion has been the unquestioning assumption that the often deep groove on the distal and medial aspect of the hook of the hamate is for the deep branch of the ulnar nerve; this is a common statement in textbooks (e.g. Frazer, 1946). Lack of appreciation of the true nature of the human anatomy, and more importantly of the progressive evolutionary change, is surprising in view of the fact that a suggestive, if not fully explanatory, illustration of the ligament was given by Weitbrecht (1742); this showed a 'reflected band' of the ligament arching around the hook of the hamate to reach the third metacarpal. This is well shown also by Poirier & Charpy (1911). Fick (1904) similarly noted the 'pars reflexa' of the ligament, and that this bundle was concealed by a ligamentous band passing from the hook of hamate to the fifth metacarpal – the 'Haken-Mittelhandband'.

These joint modifications appear to play a significant role in endowing the human hand with its unique functional capacities. The fourth and, particularly, the fifth metacarpals, freed from the buttressing influence of the hook of the hamate, achieve increased mobility, while the sellar surface for the fifth metacarpal introduces an element of conjunct rotation into flexion which, combined with the metacarpophalangeal movements noted above, produces what might be called opposition of the little finger.

The remaining basic elements of the ligamentous apparatus of the carpometacarpal junction persists in the human hand in a form virtually unchanged from that shown in pongids. In textbook accounts there is, however, a tendency for these obvious and very phylogenetically stable structures to be submerged in a welter of description of what are mere adventitious bands – morphological irrelevancies. From the prominent bony tuberosities on the trapezium (Figs. 1, 2), in front of and behind the articulation for the second metacarpal, anterior and posterior trapeziometacarpal ligaments arise. The former, lying deep to the insertion of flexor carpi radialis, attaches in part to the second metacarpal, but its major component passes in the deep groove (sometimes synovial lined) in the base of this metacarpal to a major attachment on the third. It was well illustrated by Weitbrecht (1742) and described as the L. trapeziometacarpeum volare bifurcatum by Fick (1904). The posterior ligament
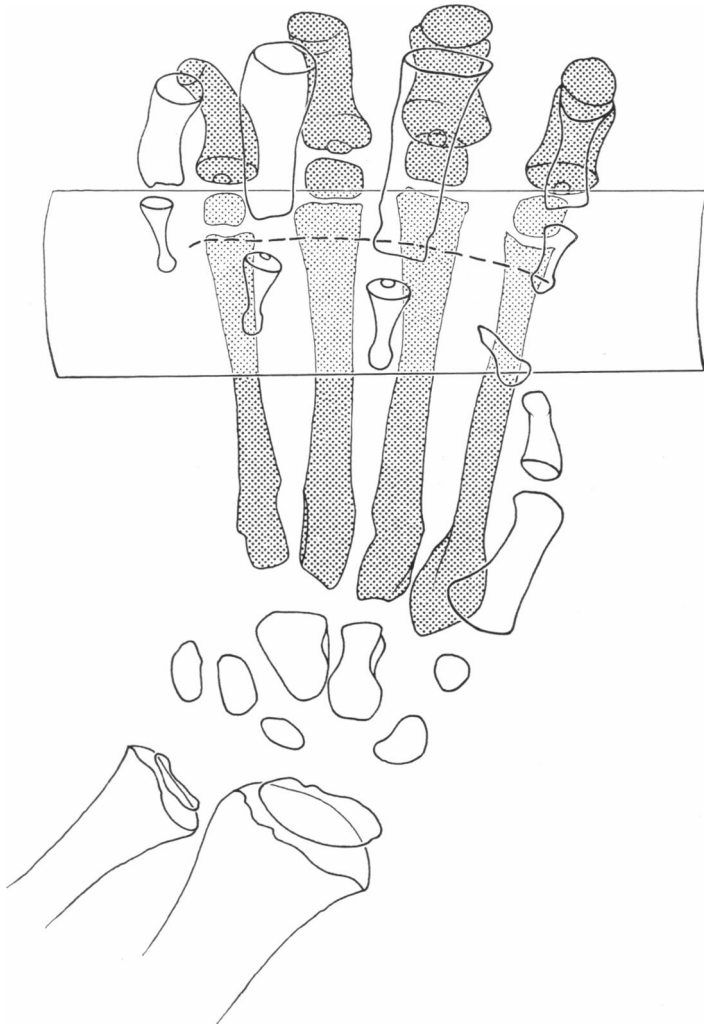
Fig. 12. The right hand of a 2 year old chimpanzee (*Pan troglodytes*) showing the positions assumed by the metacarpals and phalanges during the power grip. Drawn from a radiograph in which the distal transverse palmar crease (broken line) was indicated by a metal marker.

attaches to the index metacarpal at the radial margin of the impression for extensor carpi radialis longus and was similarly illustrated by Weitbrecht (1742) and described by Fick (1904).

The anatomy of grasping in ape and man

The anatomical features described provide some basis for interpreting the characteristic gripping postures assumed by ape and man. The demonstration of similar features in fossils may lead to better insights into the hand function of fossil hominids.

Pan troglodytes

The attitude adopted by the hand in grasping a cylindrical object (Fig. 12) reflects the relatively uncomplicated hinge action at the metacarpophalangeal joints. The transverse folding of the palm is also reflected in the transverse pattern of the skin flexion creases (Biegert, 1971). The thumb may, on occasion, play a subsidiary role by applying some counter-pressure, and it is advantageously disposed to do this by the way in which the trapezium is offset from the remainder of the distal carpal row (Fig. 9, upper).

A major factor contributing to this siting of the trapezium is the acutely wedge-shaped form of the trapezoid, which barely reaches the anterior surface of the carpus, and has its articulation with the capitate, as in all primates other than man, posteriorly located behind a thick, rounded interosseous ligament uniting the bones. It must be of functional importance that this orientation of the trapezium is not static, but is accentuated by extension of the wrist. Lewis (1972*a*, 1974) has described a rotatory movement occurring between the two carpal rows as the wrist extends. This movement is imparted by the spirally concavo-convex form of the triquetral facet on the hamate and by the architecture of the head of the capitate which is enlarged laterally, especially in its anterior portion, giving the bone an exaggeratedly 'wasp-waisted' appearance (Fig. 13). Posteriorly, this waist or neck is formed by an articular surface which is confluent below with a facet for the trapezoid; anteriorly it forms a deeply undercut, non-articular groove. Dorsiflexion (extension) of the wrist is accompanied by a rotatory movement at the midcarpal joint. When this movement is completed with full extension, the joint is in the close-packed, maximally congruent position; the scaphoid fits firmly on to the articular neck of the capitate, its anterior portion (bearing the facets for trapezoid and trapezium) becoming firmly embedded beneath the bulbous capitate head, and the triquetral is closely fitted into the posterior part of its spiral hamate facet. This mechanism is an especially clear-cut example of a basic principle in joint mechanics which has been thoroughly discussed by MacConaill (1953) and MacConaill & Basmajian (1969), namely that at all non-pivot joints the characteristic or habitual movement is a composite one involving some degree of rotation, and such rotation, called conjunct rotation, is most marked in joints with concavo-convex surfaces, where it is effective in screwing the bones together into a locked position.

When first described it was suggested that this mechanism in *Pan* seemed admirably adapted to meet tensional forces applied to the limb during forelimb suspensory posturing. This viewpoint has been challenged by Preuschoft (1973*a*). This author has been greatly preoccupied with emphasizing that the skeletal system, even in suspensory attitudes, is subjected to compressive forces by the musculature (Preuschoft, 1973*b*), but in this he seems to have underplayed the role of close-packing of joints. The midcarpal mechanism would, of course, convert tensional forces on the limb as a whole into compressive ones at the joint interfaces. The view of the primacy of suspension in perfecting this mechanism has been attacked with extraordinary acrimony by Tuttle (1974), who much prefers to see it as a specialization for knuckle-walking. In fact, Lewis (1974) recognized its probable value here and suggested that it was pre-adaptive for this activity. If it was evolved *de novo* as an evolutionary
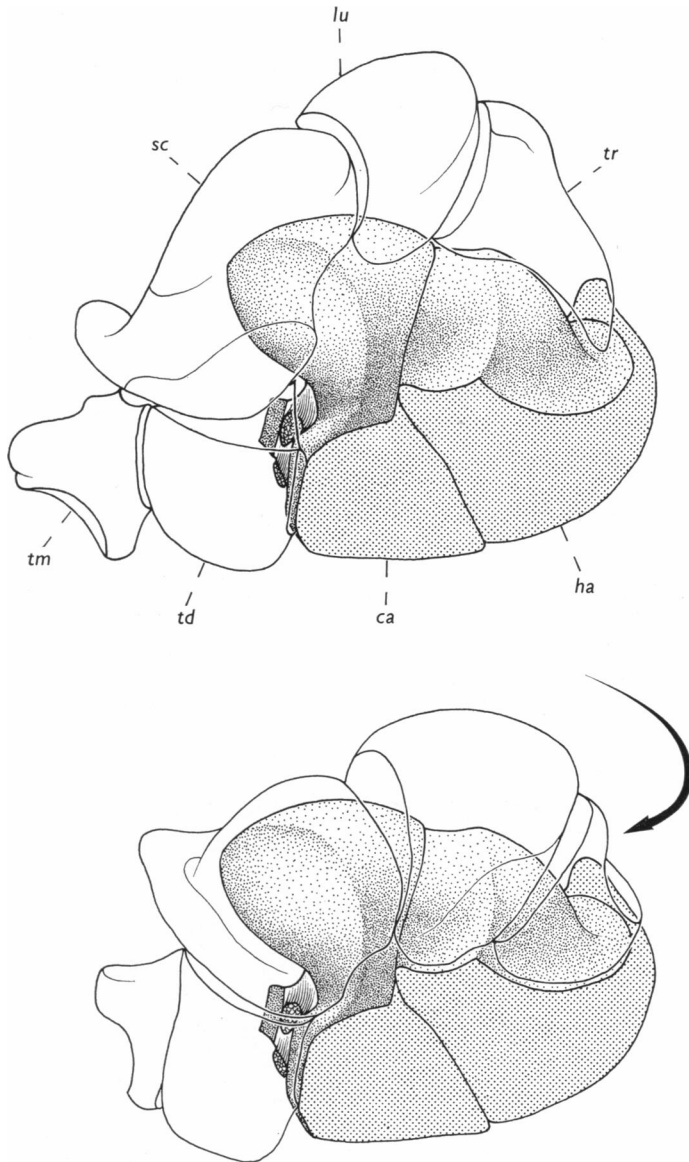
Fig. 13. The midcarpal mechanism in *Pan troglodytes*, drawn from the cartilage-clad bones of the left wrist of a wet specimen. Above, the capitate (*ca*) and hamate (*ha*) are viewed from behind with the bones of the proximal row – scaphoid (*sc*), lunate (*lu*), triquetral (*tr*) – and the trapezoid (*td*) and trapezium (*tm*) superimposed in outline upon them in the position occupied in flexion. Below, the same bones are shown in the positions taken up on moving into full extension with the arrow indicating the direction of conjunct rotation of the proximal row.

expedient associated with knuckle-walking it is difficult to appreciate why gorillas, the most committed of knuckle-walkers, should have a capitate with the waist largely expanded by bony deposition in a manner analogous to that of man. It would seem that anyone seeking real knuckle-walking specializations in the carpus need look no further than the great dorsal buttress developed on the gorilla trapezium.

The midcarpal rotational movement clearly forces the trapezium anteriorly, accentuating the carpal arch and increasing the offset location of the thumb, which is then in a position perhaps to exert some counter-pressure, but is at least carried out of the way of structures traversing the palm.

The gripping mechanism in other pongids appears to be similar in essentials. In hylobatids the grasp is even more hook-like (Tuttle, 1972). Lorenz (1974) called this the 'comb grip' and noted how the thumb may be 'melted' into the side of the palm during this activity. The flat form of the gibbon palm, a consequence of its flat carpal arch, explains why the simplest of hinge movements at the metacarpophalangeal joints meets the needs of the gibbon grasping action. In other pongids some rotation at the joints of the marginal fingers on the asymmetrical heads of the index and minimus metacarpals presumably correctly aligns the fingers.

Homo sapiens

The gripping posture evidenced by man in taking hold of a cylindrical object (Fig. 14) illustrates well the specializations involved. This attitude is the power grip of Napier (1956), and it contrasts markedly with the apes in the oblique orientation of the object across the palm. This is a consequence firstly of the attitude taken up by the second to fourth metacarpals, which are progressively deviated volarly in passing from the radial to the ulnar side. The immobile metacarpal of the medius is in the neutral position; the metacarpal of the index is apparently slightly extended and exorotated; the metacarpals of the annularis and minimus (especially the latter) are flexed towards the palm and exorotated. These movements are undoubtedly dependent upon the modifications evolved at the human second and fourth and fifth carpometacarpal joints.

The metacarpophalangeal joints make their unique contribution to the overall posture. That of the proximal phalanx of the index finger is extended, ulnar deviated, and exorotated, as in Figure 7 A. The remaining proximal phalanges are progressively flexed so that that of the minimus takes up the position of flexion, ulnar deviation, and exorotation as in Figure 8 B. The overall result is that an oblique gutter is formed across the palm and this is reflected in the manner in which the palmar skin is folded with the creation of a (usually) obliquely disposed distal 'transverse' skin crease (the palmist's 'line of heart').

Some counter-pressure is exerted on the ulnar side of the hand by the hypothenar fat pad, the skin here being stabilized by the palmaris brevis muscle (Kirk, 1924).

On the radial side counter-pressure is exerted by the thumb. It is here that the changes in the human carpal arch seem to assume particular significance, for, with the trapezium laid back towards the plane of the remainder of the distal carpal row (Fig. 9, lower), the extended, adducted and laterally rotated thumb is well disposed to exert counter-pressure against the cylinder which has the index finger curled around it. In this position the lateral ligament of the carpometacarpal joint is taut,
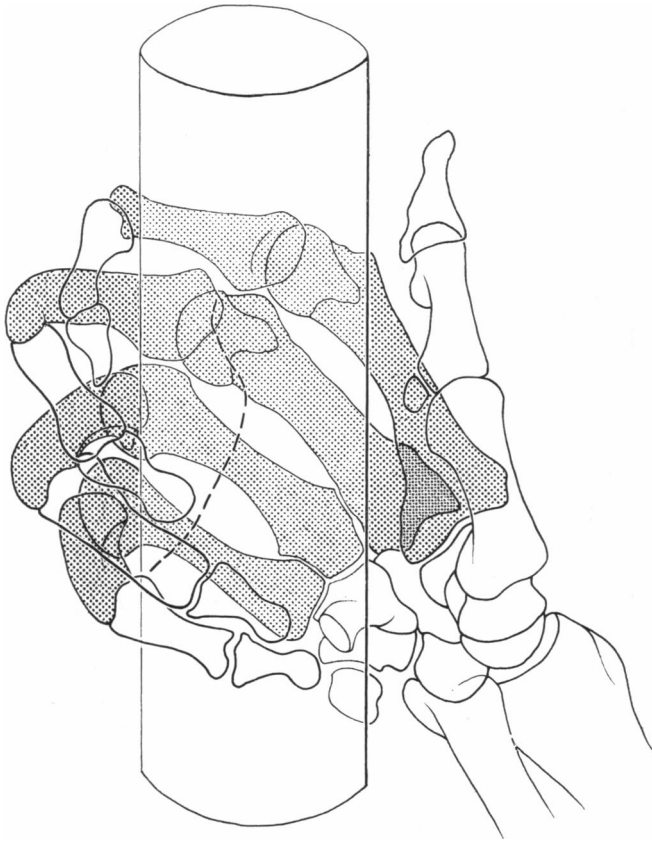
Fig. 14. The right hand of *Homo sapiens* showing the positions assumed by the metacarpals and phalanges during the power grip. Drawn from a radiograph in which the distal transverse palmar crease (broken line) was indicated by a metal marker.

a fact amply attested to by radiographs which show the wide separation between its attachments; the joint is then in one of its close-packed positions, as noted by Napier (1955) and by Kuczynski (1974). The significance of the human elaboration of this lateral ligament, as a partial sequestration of the ape posterior oblique ligament around on to the broadening lateral surface of the trapezium, then becomes apparent.

It seems possible also to put forward a tentative hypothesis explaining the unique human pattern of the articulations between the capitate and trapezoid, which has been described in detail by Lewis (1973). The primitive ape disposition of a posterior articulation between those bones (Fig. 9, upper) has been replaced in the human carpus by a completely new diarthrodial articulation anterior to the thick, rounded interosseous ligament between them (Fig. 9, lower). In the power grip (Fig. 14) it is suggested that considerable compressive forces may be transmitted from the first metacarpal base to the trapezium and thence across the expanded anterior part of the trapezoid to the capitate. The enlargement of the volar aspect of the trapezoid, readjusting the 'set' of the trapezium, and the establishment of a new anterior

diarthrosis with the capitate can then be interpreted as morphological markers of the human power grip.

In the power grip the wrist is typically ulnar deviated and in a neutral position. It has been shown by Wright (1935) that during ulnar deviation about 6° of the movement occurs at the midcarpal joint and the scaphoid is then swung into the long axis of the forearm; it is likely that this further moves the trapezium, and thus the base of the thumb, back towards the plane of the forearm. On passing to the precision grip the ulnar deviation is generally corrected and extension of the wrist is typically exaggerated. This raises the important question whether midcarpal conjunct rotation (as occurs in the chimpanzee wrist) plays a role in the human precision grip. Attention was drawn to the chimpanzee wrist mechanism by the observation of MacConaill (1941) that during wrist extension the human triquetrum is screwed against the lunate and scaphoid, this movement being dictated by the spiral form of its articulation with the hamate. Interpretation of the 'waisted' form of the chimpanzee capitate and of the rotatory movement between the two carpal rows was then fairly obvious; this illustrates the value of comparative observations, for fundamental morphological features or functional mechanisms are often highlighted and seen almost in caricature. There can be no doubt that a mechanism of conjunct rotation such as that shown in Figure 13 also operates in man, modified somewhat by filling out of the lateral indentation of the capitate so that 'waisting' in the human bone is less obvious (Lewis, 1973). This expansion of the capitate waist limits the embracing movement of the scaphoid about the capitate head and causes the bones of the proximal row to splay apart. The individual movements of the lunate and scaphoid described by Kauer (1974) are readily interpretable as components of this conjunct rotation considered in isolation.

Conjunct rotation accompanying extension is obviously advantageous in setting up the carpus for the precision grip, for the scaphoid will then carry the trapezium in a palmar direction. That this actually occurs is quite detectable in still radiographs, the pisiform and the tubercle of the scaphoid providing unequivocal markers for the movements of the proximal carpal row. Even more convincingly this is strikingly shown in a cineradiographic film, now something of a classic, by Barclay & Seddon (1945), although not there commented upon.*

From this improved disposition the thumb can move into opposition by the diadochal movement of abduction and flexion, combined with conjunct rotation in the sense of pronation. Clearly both anterior and posterior oblique ligaments are then tightened and the joint is in its second close-packed position.

When the more ulnar digits are involved in this grip they occupy positions similar to those attained in the power grip, and if the index finger is involved with them (as in grasping a small spherical object with the fingers) it moves toward a position of flexion, combined with pronation and abduction, as in Figure 7B. In grasping a small object between index finger and thumb, the index often is disposed rather as in the power grip (Fig. 7A).

* *Movements of Joints Demonstrated by Cineradiography*. From The Nuffield Institute for Medical Research and The Nuffield Department of Orthopaedic Surgery, Oxford. Available on loan from the B.M.A. Film Library.

Lower Pleistocene hominid fossils

The findings described above are clearly applicable to the gradually accumulating array of hand bones of emergent hominids, which have been considered either as members of the genus *Australopithecus* or, in some cases, attributed on rather dubious grounds to *Homo*. Attribution to any particular genus or species is hazardous, and seems to have been determined more by site of recovery than by morphological insights.

The Sterkfontein capitate (*TM*1526)

The interpretations, in terms of hand function, have been described in detail (Lewis, 1973) and will not be fully reiterated here. Some mention is necessary, however, because previous conclusions, well entrenched in the literature, were based upon inadequate and often incorrect comparative and human morphological data, yet seem to have strongly influenced interpretations of other fossils. Thus Clark (1947, 1967) stated that the bone had 'a very human appearance' and that 'the capitate and the adjacent bones of the hand were less free in *Plesianthropus* than in Europeans, but much more free than in the hand of modern anthropoid apes'. It can now, however, be seen that these views were based on incorrect anatomical assumptions and thus have no clearly defensible logical basis. In fact, this fossil shows quite a marked degree of 'waisting', the trapezoid articulated posteriorly with it, and the second metacarpal seemingly articulated with it, by large anterior and small posterior facets separated by an interosseous ligament. It thus possessed, but slightly modified, the essential biomechanical attributes shown by *Pan*, but had not achieved to any great extent those morphological correlates of human hand function described above.

The fossil came from the Sterkfontein lower breccia, type site, and was not associated with tools, although stone artefacts have been found at the Sterkfontein extension site. It was originally attributed to '*Plesianthropus transvaalensis*' by Broom & Schepers (1946); however, only gracile australopithecines have been obtained from this site and the fossil is now usually classified as *Australopithecus africanus*.

The Swartkrans fifth metacarpal (*SKW*14147)

This recently discovered fossil, a left fifth metacarpal, has been the subject of only one description and interpretation (Day & Scheuer, 1973). The functional morphology of extant primates described above fails to sustain the conclusions reached by these authors and, in fact, appears to dictate a very different interpretation.

The head (Figs. 19, 20) possesses no knuckle-walking ridges and is asymmetrical, being somewhat bevelled off dorsally on the ulnar side. Volarly, there are grooves for the glenoid plate (and perhaps sesamoids) which delimit marginal flat-sided elevations over which the collateral ligaments would ride. The elevation on the ulnar side is somewhat larger and prolonged further proximally. The asymmetry of the head is of the same order as that found in chimpanzee specimens lacking knuckling ridges. Although the head is broader, as it is in *Homo sapiens*, the asymmetry of the head falls short of that usually seen in man and the ulnar articular elevation also lacks the considerable cam-shaped enlargement shown in man. The functional mechanism is
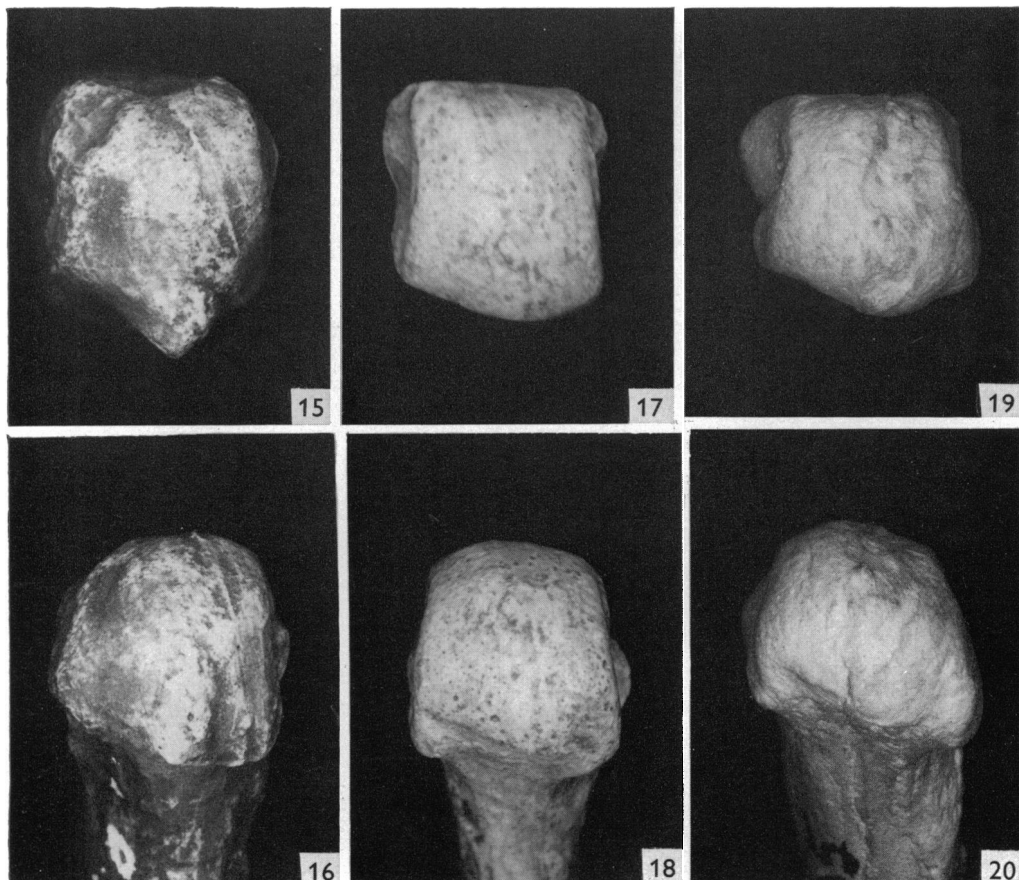
Figs. 15–20. Metacarpal heads viewed from standardized positions: above, from directly distally; below, from an angle of 45° distoventrally.

Figs. 15 and 16. The cast of the Swartkrans first metacarpal (SK84). × 3.

Figs. 17 and 18. The cast of the Swartkrans fourth metacarpal (SK85). × 3.

Figs. 19 and 20. The cast of the Swartkrans fifth metacarpal (SKW14147). × 3.

clearly as described above, with some minor advance along the path to *Homo* from the condition shown in *Pan*.

Day & Scheuer (1973) assumed that the asymmetry of the head was associated with an enhanced range of abduction of the minimus and a consequent broadening of the hand, and in this they likened it to *Homo sapiens*. Whilst apparently plausible on cursory inspection of a dry bone, this view, in fact, reflects a misinterpretation of the biomechanical effects of this shearing off of the dorso-ulnar part of the head. These effects have been explained in some detail in this paper, and can be readily verified by anyone having access to a ligamentous human preparation.

The architecture of the base of the bone (Figs. 21–23) is immediately evocative of the arrangements in *Pan* (which as noted above, conserves here much of the basic
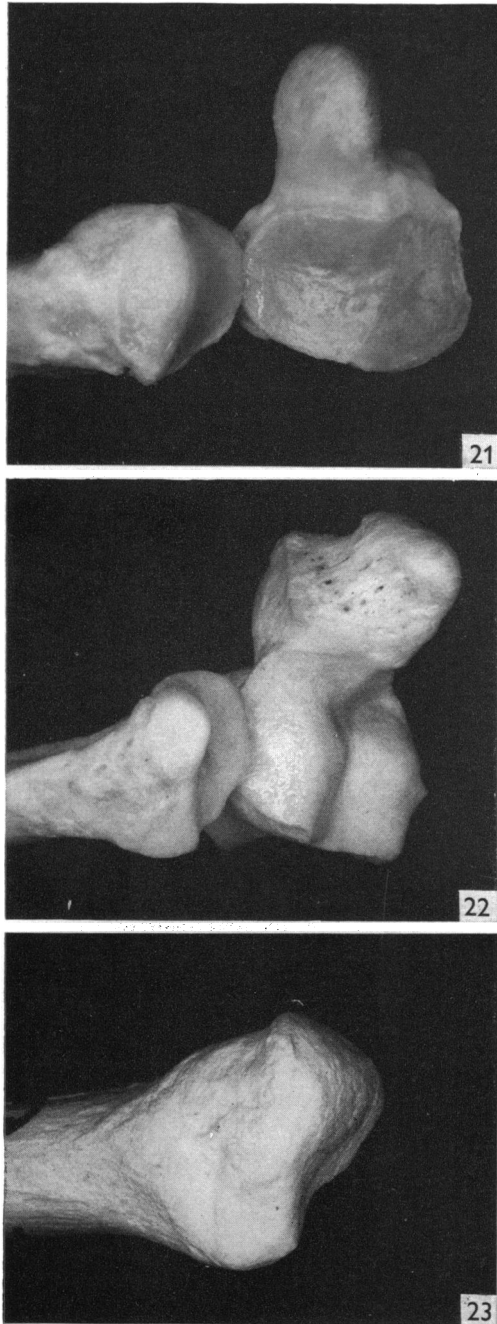
Fig. 21. The base of the left fifth metacarpal of *Homo sapiens* viewed from the radial side, with the corresponding hamate rotated away from articulation with it. × 2.

Fig. 22. The left fifth metacarpal and hamate of *Pan troglodytes* (B.M. 1948.10.25.2) orientated in a manner comparable to that of the bones shown in Fig. 21. × 2.

Fig. 23. The base of the cast of the Swartkrans fifth metacarpal (SKW14147) viewed from the radial side, in a position comparable to that of the bones shown in Figs. 21 and 22. × 3.

primate structure) and lacks the complex specializations characteristic of *Homo sapiens*. The base presents a concave dorsal portion, for articulation with the body of the hamate, and a deflected volar convex lip which is obviously for articulation with the hamate hook; as described above, only the former of these areas is strictly homologous with the whole hamate facet on the human metacarpal. Clearly the base of the bone entered into a stable articulation with the hamate, braced ventrally by its hook, as in the chimpanzee, but contrasting markedly with that of man. Day & Scheuer (1973) speculated about the joint surface being concavo-convex (this is true in the sense that there are concave and convex component areas) and that while it 'does not conform to a true saddle' it also 'provides for rotatory movement at the base'. These are clearly quite fundamental misconceptions about the anatomical arrangements, and are quite untenable. To conclude, as did these authors, that in its various features the fossil indicates 'a mode of hand function not unlike that of modern man' is inexplicable. Indeed, prime morphological markers indicate hand function more like that of apes, without, of course, such specializations as knuckle-walking metacarpal shelves. There is nothing to indicate that the unique human specializations of the ulnar side of the hand had been acquired. Day & Scheuer (1973) further concluded from a univariate metrical comparison with human bones that the fossil differed little, if at all, from *Homo sapiens*. None of the measurements, however, reflected the most functionally important morphological markers present in the fossil, and this provides a sobering example of the pitfalls inherent in purely metrical analysis – whether univariate or multivariate – when adequate background morphological data are lacking.

The first metacarpal from Swartkrans (SK84)

This metacarpal of the left pollex was described by Broom & Robinson (1949b) and subsequently by Napier (1959).

As noted above, the base of the first metacarpal is not well endowed with functional markers which might be used as a measure of human uniqueness. The articular surface of the fossil is of course saddle-shaped, and as Napier (1959) correctly noted, its mediolateral convexity exceeds that of man and approximates that of the Pongidae. To this may be added the functionally significant point that the lateral extension of the articular surface appears to occupy the area which in man is non-articular for the lateral ligament (Fig. 1). That the articular surface may not have retreated here is perhaps presumptive evidence of a lack of specialization of the lateral part of the posterior oblique ligament into a descriptive lateral ligament, and would thereby indicate functional affinities with the Pongidae.

The head of the bone has a strange beaked form (Figs. 15, 16) which has greatly perplexed observers. Not surprisingly, and no doubt correctly, this has suggested the presence of large sesamoids. Equally predictably, this has almost inevitably been followed by the inference that large intrinsic muscles, especially adductor pollicis (Napier, 1959), were present and that the thumb, therefore, was of considerable muscularity and prehensile power. Whilst this conclusion on other grounds may be correct, it does not logically follow here, for, as stated above, the sesamoids are ossifications within the glenoid plate, acting as strengthening for its margins. Also, quite unjustifiably, Broom & Robinson (1949b) stated: 'as we have evidence of two

large sesamoids it seems likely that the thumb ... was a useful clasping organ and able to manipulate tools and weapons'.

The head shows a mild degree of asymmetry, being bevelled off dorsally on the radial side. In no way can this be considered as a specialization for increased abduction in extension (Napier, 1959). Rather the biomechanics are clearly as described above for the index: abduction with medial rotation (pronation) would accompany flexion, thus compounding similar movements of opposition at the carpometacarpal joint. The leading role of the glenoid plates in metacarpophalangeal movements was referred to above, and it was noted that as they track up over the metacarpal head they effectively drag the phalangeal base in their wake. The curious beaked character of SK84 then becomes clearer and, paradoxically, insight is obtained by considering the analogy of the mechanism at the hallucial metatarsophalangeal joint. If this joint be examined in a wet specimen of *Pan troglodytes* (or indeed in *Homo sapiens*) it is seen that the cartilage-clothed metatarsal head is quite strikingly reminiscent of that of SK84. The functional import is also easy to determine in the chimpanzee foot: the grooves on either side of the central beak guide the sesamoid-reinforced margins of the glenoid plate in an arcuate course over the head of the metatarsal. This movement clearly reinforces the similar rotatory movement at the tarsometatarsal joint (Lewis, 1972*b*) and obviously increases the efficacy of the grasping hallux.

It is suggested that a similar mechanism was operative at the joint of SK84. Thus, a picture emerges of what might have been the retention of a quite basal hominoid type of thumb action in which a carpometacarpal joint not unlike that of modern pongids (but lacking the rather subtle specializations found in man) and possessing similar function, had its movements enhanced by those occurring at the metacarpophalangeal joint. It may be reasonably inferred, however, that the fossil thumb lacked those specializations found in living pongids which reflect diminished functional importance, such as the reduction of the long flexor tendon.

A multivariate analysis based on 12 measurements was performed on this fossil by Rightmire (1972). The results were unsatisfactory and ambiguous and this is not surprising when it is realized that none of the measurements chosen reflect features of great functional importance such as those noted here. Again this illustrates the essential sterility of this approach, at least until adequate morphological insights are available.

The Swartkrans fourth metacarpal (SK85)

This specimen, lacking the base but preserving the head, was described by Napier (1959) as a left fourth metacarpal and was attributed by him to '*Telanthropus*'.

No knuckle-walking ridges are present, only a hint of head asymmetry, and only rudimentary volar grooves and limiting rims (Figs. 17, 18). It thus preserves a fairly unspecialized character consistent with an essentially hinge-like movement of flexion such as occurs in the metacarpophalangeal joints of *Pan* (which, however, possesses knuckle-walking ridges); this arrangement persists in the human fourth metacarpal (though volar articular prolongations are usually larger than those of the fossil). The lack of progressive modifications in the human fourth metacarpal makes it a rather uninformative bone. The fossil is clearly hominoid, but there seem to be no compelling grounds for referring it to '*Telanthropus*' rather than to *Australopithecus*.
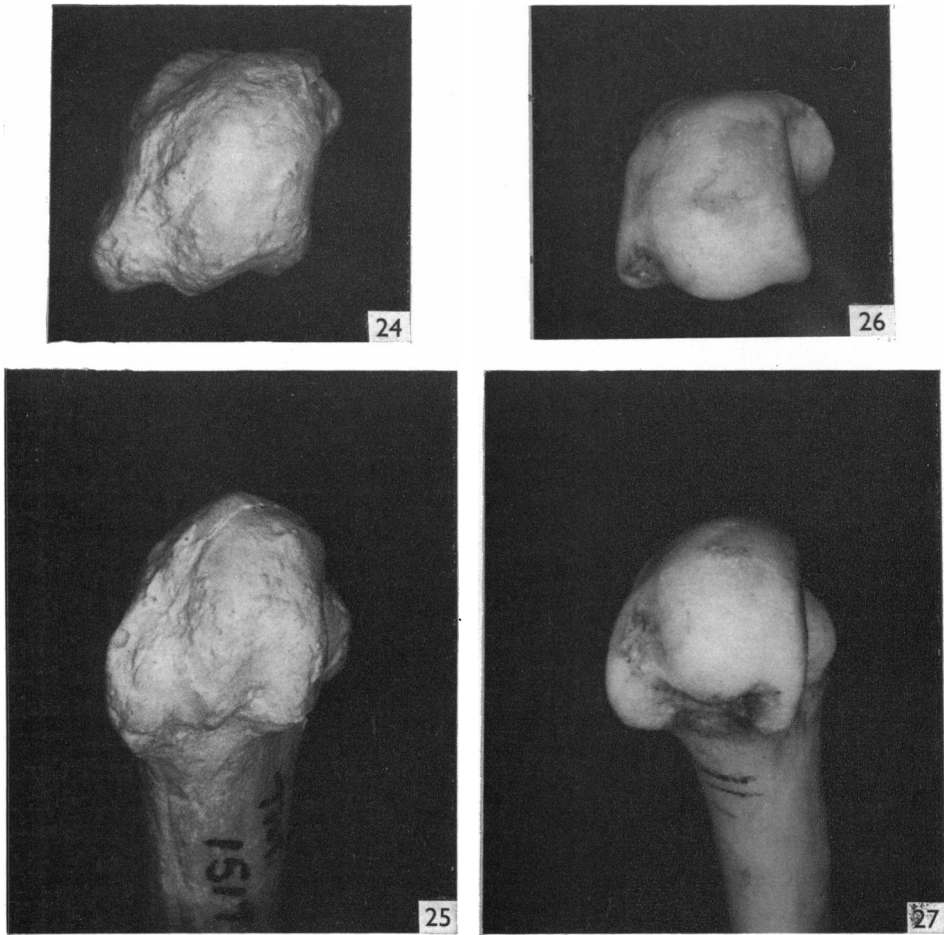
Figs. 24–27. Metacarpal heads viewed from standardized positions: above, from directly distally; below, from an angle of 45° distoventrally.

Figs. 24 and 25. The cast of the Kromdraai left second metacarpal (TM1517h). × 3.

Figs. 26 and 27. The left second metacarpal of *Papio anubis* (B.M. 1901.8.9.23). × 3.

The Kromdraai second metacarpal (TM 1517) *and associated proximal phalanx*

The fossil metacarpal shows a curious assemblage of features which, in the light of the observations presented here for extant primates, seem to be irreconcilable with its supposed hominoid status. The head is bevelled off dorsolaterally as one would expect of a left human index metacarpal (Figs. 24, 25). On its volar aspect it is markedly fluted, presenting a prominent median crest flanked by grooves. This has prompted the inevitable speculation about sesamoids and the presence of strong intrinsic flexor muscles (Robinson, 1972). The margin of the sesamoid groove on the presumptive radial side is not especially large and cam-like, as one would expect if it were equivalent to the other part of the human morphological complex. The head of

the metacarpal, in fact, appears to conserve an essentially pre-hominoid morphology reminiscent of that seen in extant cercopithecoids (Figs. 26, 27).

The composite structure seems quite out of line with the theme developed in this paper. The assumption has been that median cresting of the metacarpals (except the first) was lost early in hominoid evolution – it is absent in the Miocene ape *Dryopithecus (Proconsul) africanus* – and certainly had been virtually suppressed by the time of the emergence of the hominids. It has further been suggested that in these protohominids dorsal bevelling was already present in the index and minimus metacarpal heads, and that the human condition was achieved by some accentuation of this feature coupled with the elaboration of single marginal volar cams in each of these digits.

When Broom (1942) first described this bone he voiced some doubts about its apparent baboon-like form, but rejected these and plumped for its really being from the hand of '*Paranthropus*'. In this he was largely swayed by its very close association within a cubic foot of bone breccia with the type skull of '*Paranthropus*' and by the fact that no giant fossil baboons (such as *Dinopithecus ingens*, found elsewhere in the Transvaal) were then known at Kromdraai. He clearly had lingering doubts, however, and suggested that if ever teeth of *Dinopithecus* should be discovered at Kromdraai the question as to whether these hand bones are really '*Paranthropus*' might require revision.

By the time of the publication of the definitive account (Broom & Schepers, 1946) all lingering doubts appeared to have vanished – the metacarpal effectively, for Broom at least, became that of '*Paranthropus*'! This fossil has had a quite significant influence on views on human evolution, for its discovery prompted Broom (1942) to relinquish the views of Gregory (1934) stressing man's affinities with the apes and espouse instead the idea of Osborn (1930), who argued for a derivation of the hominid line from a much earlier horizon of primate evolution. Interestingly, shortly afterwards a massive fossil baboon was found at Kromdraai and described as *Gorgopithecus major* by Broom & Robinson (1949a); the question of the hand bones was not, however, re-opened.

The close association of the metacarpal with the '*Paranthropus*' type skull has proved a compelling reason for subsequent authors (e.g. Robinson, 1972) to accept the hominid authenticity of the metacarpal.

What has been conveniently forgotten, however, is that another small proximal phalanx was found in contact with the index metacarpal, and this Broom (1942) and Broom & Schepers (1946) unhesitatingly attributed to the small fossil baboon '*Parapapio*' *augusticeps* (re-designated *Papio augusticeps* by Freedman, 1957) which is common at the Kromdraai site. This attribution has never been questioned and, indeed, a portion of the frontal bone of the same baboon species was also found in the same block of matrix. The presence of undoubted fossil baboon remains in the same cubic foot of breccia surely demolishes any obligation to believe in a taxonomic affinity between the skull and metacarpal merely on the basis of the close association of their sites of discovery.

Broom (1942) was hindered in his interpretations by his evident unfamiliarity with the functional anatomy of the baboon metacarpophalangeal joints. Examination of a wet specimen (*Papio papio*) shows that these joints are subtly modified to cope with

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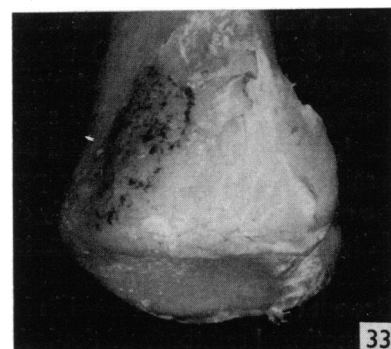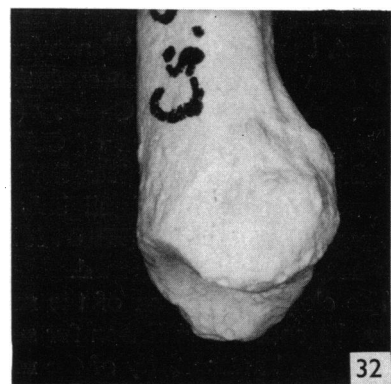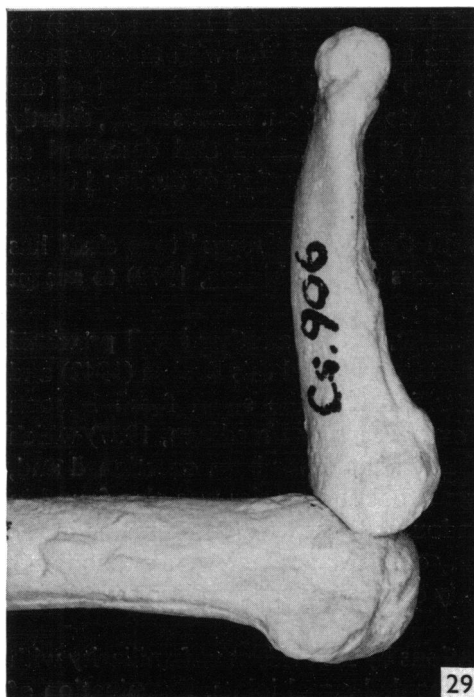
the digitigrade method of walking. The bases of the proximal phalanges are scooped out dorsally allowing them to reach a close-packed position at about 90° hyperextension on the metacarpal heads, whose distal ends in this position are covered by the sesamoid-containing glenoid plates. The heads of the metacarpals of the index and minimus are dorsally bevelled in the usual fashion, and, perhaps even more importantly than in plantigrade animals, this aligns the digits and correctly orientates their volar surfaces to the substrate below; this is additionally helped by the fact that the distal extremities of the four postaxial metacarpals are almost in line (Etter, 1973). The remodelling of the baboon phalangeal base gives the impression, when seen in side view, that the dorsal corner has been sheared off; this, in fact, was strikingly shown in illustrations of the supposed 'Paranthropus' phalanx by Broom & Schepers (1946), but clearly failed to arouse the appropriate scepticism (Figs. 30–33). Articulation of the fossil metacarpal and phalanx (Figs. 28, 29) leaves little doubt that they belong to a large fossil baboon, possibly *Gorgopithecus major*. There have, however, been indications (though not fully proven) of the presence at Kromdraai of the even larger *Dinopithecus ingens* (Freedman, 1957), and the fossils may appertain to that species. Regardless of this nicety there now seem adequate grounds for removing these specimens from consideration in discussions of hominoid hand evolution.

The hand bones from Bed I, Olduvai Gorge (OH7)

These bones have been described by Napier (1962) and have been tentatively attributed to the taxon '*Homo habilis*'. The only available specimens which are interpretable in the light of the present study are a right trapezium, a right scaphoid and the base of a right second metacarpal.

Trapezium. The fossil is almost complete except that the tuberculum (crest) is broken off. The distal articular surface is concavo-convex but broader in dorso-volar extent than that of *Pan* and approximates *Gorilla* and *Homo sapiens* in this feature (Figs. 35, 37, 39 and 41). Adjacent to the radial end of its dorsal border is a dorsal tubercle, obviously for a posterior oblique ligament. This prominence (Fig. 40) immediately adjoins the border as in *Pan* (Fig. 36) and it is not truncated and separated from the border leaving an area for the origin of a lateral ligament, as in man (Fig. 34); the lack of elaboration of this ligament can tentatively be inferred.

The dorsal surface (Figs. 34, 36 and 40) shows well the dorsal tubercle, adjacent to the articular surface, for the posterior oblique ligament. Also, as in man and *Pan*,

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Fig. 28. The left second metacarpal and its corresponding proximal phalanx of *Papio anubis* (B.M. 1901.8.9.23) articulated in hyperextension and viewed from laterally. × 2.

Fig. 29. The casts of the Kromdraai left second metacarpal and associated proximal phalanx (TM1517h and TM1517i) articulated and viewed as in Fig. 28. × 2.

Figs. 30–33. The bases of proximal phalanges of left index fingers, in each case viewed from laterally.

Fig. 30. *Papio anubis* (B.M. 1901.8.9.23). × 3.

Fig. 31. The cast of '*Parapapio*' *augusticeps* (TM1517j). × 3.

Fig. 32. The cast of the Kromdraai proximal phalanx, attributed to '*Paranthropus*' (TM1517i). × 3.

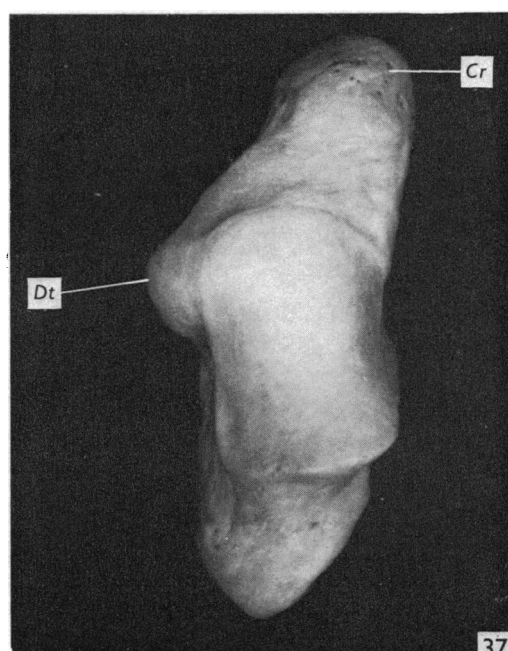Fig. 33. *Pan troglodytes* (B.M. 1924.8.6.1). × 3.
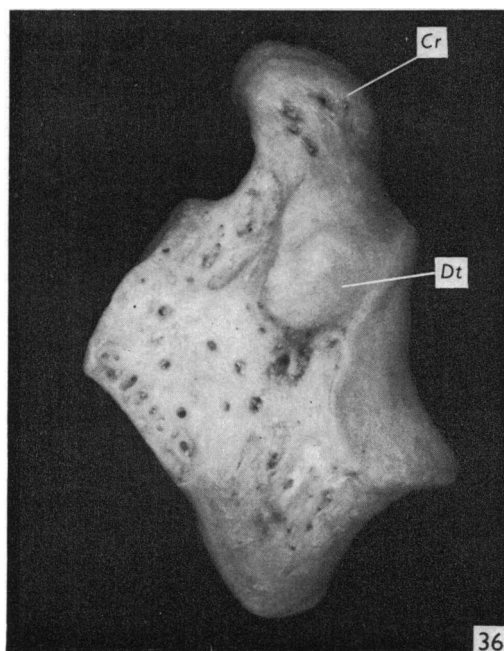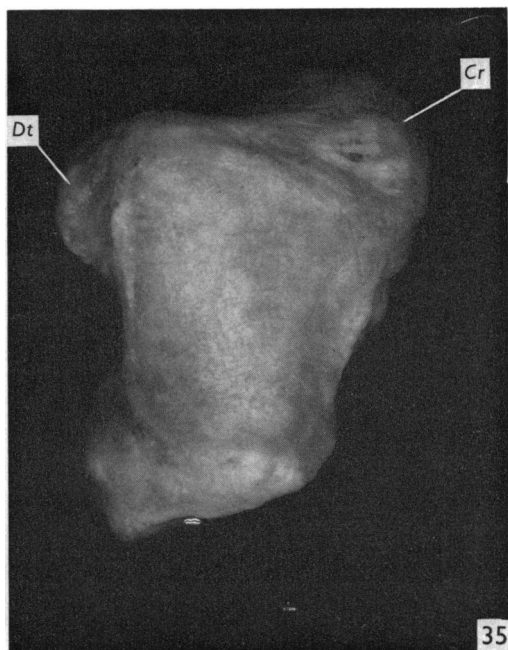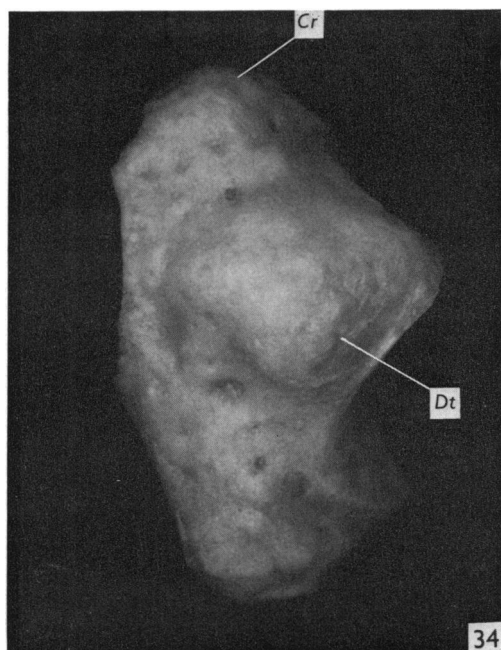
Fig. 34. The right trapezium of *Homo sapiens*, viewed from dorsally. *Cr*, tubercle (or crest); *Dt*, dorsal tubercle. × 3.

Fig. 35. The bone shown in Fig. 34, with labelling as before, viewed from distally. × 3.

Fig. 36. The right trapezium of *Pan troglodytes* (B.M. 1948.10.25.2) viewed from dorsally. *Cr*, tubercle (or crest); *Dt*, dorsal tubercle. × 3.

Fig. 37. The bone shown in Fig. 36, with labelling as before, viewed from distally. × 3.

there is a further tubercle, medially situated, for the carpometacarpal ligament reinforcing the back of the joint with the second metacarpal.

The lateral surface of the bone is expanded when compared with the ape condition, but indications are that the situation and form of the missing crest were more like *Pan* than man.

It has been noted that the important human specialization by which the trapezium has been re-orientated was largely achieved by remodelling of the trapezoid and capitate and of the articulation between them. Neither of these bones is available in the Olduvai find, but a reasonable indication of the 'set' of the trapezium can be deduced, since there is available the damaged base of a second right metacarpal which fortunately conserves the area of insertion of extensor carpi radialis longus and the adjacent articulation for the trapezium. The second metacarpal facet of the trapezium is a direct continuation of that for the trapezoid, with only slight angulation between the two, in *Pan* (Fig. 9, upper); in man, with splaying apart of the carpal arch, the metacarpal facet on the trapezium, is almost at right angles to the trapezoid one (Fig. 9, lower). In this regard the fossil trapezium is more like that of the apes; when articulated with the second metacarpal this impression is reinforced (Figs. 42–45).

Napier (1962) mentioned in regard to the fossil that 'the evidence provided by the other articular surfaces indicates that its "set" in the carpus was unlike that found in modern man and similar to the condition in *Gorilla*'. He did not, however, provide any reasoned support for this statement.

Scaphoid. Because of the rotatory mechanism at the midcarpal joint (Fig. 13) the scaphoid should provide evidence of the orientation of the trapezium with respect to the other distal carpal bones. Thus, in *Pan*, the bunched up character of the distal carpal row means that the trapezoid and trapezium facets on the scaphoid closely adjoin the margin of the capitate surface, and the tuberosity of the bone is free from articulation and presents as an upturned beak. In *Homo sapiens*, in contrast, the distal carpals are splayed apart radially and the facet for the trapezium extends out to the under surface of the tuberosity of the scaphoid.

In the fossil the tip of the tuberosity is broken off, but there are strong indications that it had the beak-like character, and that the articulations for the trapezoid and trapezium bore more resemblance in their location to *Pan* than to *Homo sapiens*.

Capitate. This bone, a left-sided one, was found at the same site as those considered above, but clearly did not belong to the same hand. Its potentially informative lateral surface was badly damaged. It has been considered by Lewis (1973). Little can be said of it except that it certainly bore no more of the characteristics of hominization than did the Sterkfontein capitate. There is no discernible reason for the pronouncement by Napier (1962) that it 'is generally more *sapiens* than ape-like'.

Function in the hand of OH7

Considerable play has been made of the 'set' of the trapezium as a distinguishing feature between pongids and man, but the functional import of this has been unspecified, or at least vague. The implication appears to be (Napier, 1962) that the human arrangement is an essentially negative feature and that the 'set' in pongids indicates a deep carpal tunnel, and thus strong, long finger flexors.
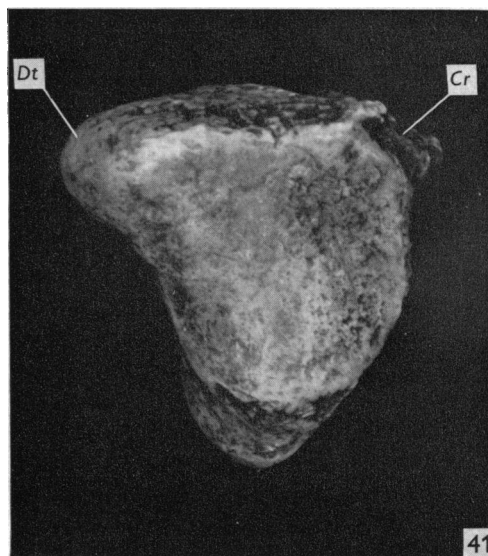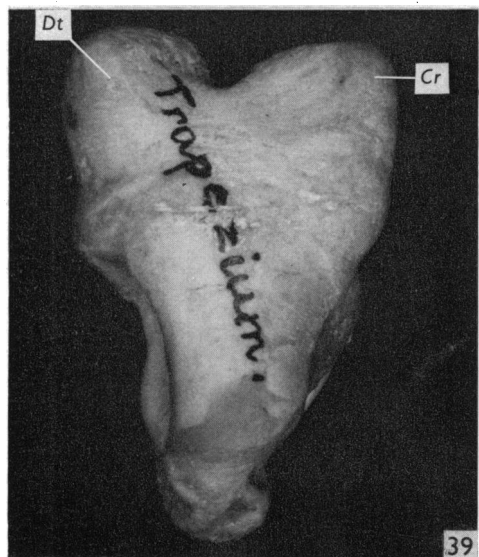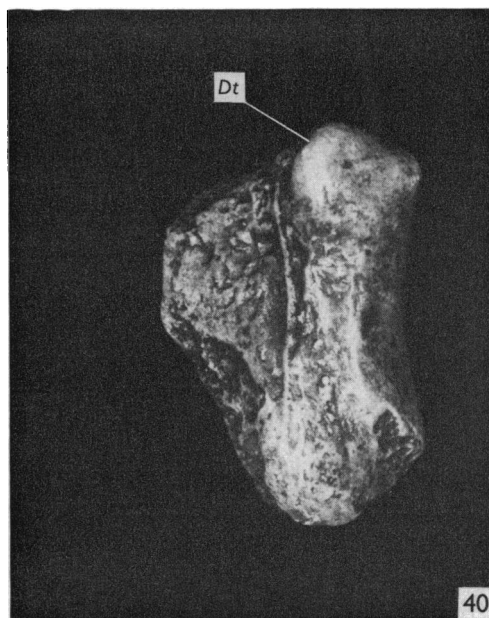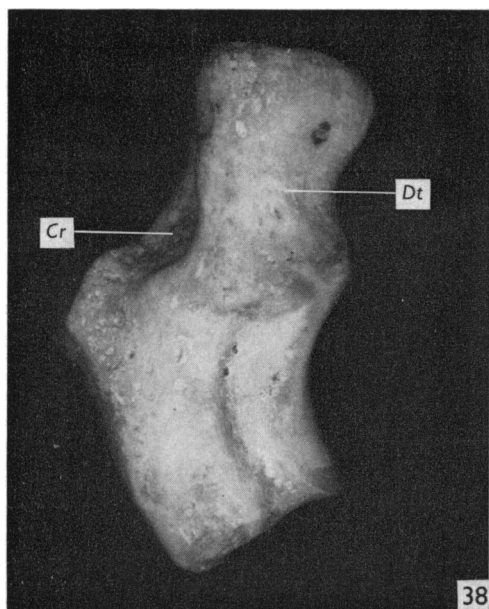
Fig. 38. The right trapezium of *Gorilla gorilla beringei* (B.M. 1961.4.5.1) viewed from dorsally. Seen from this aspect, the greatly enlarged dorsal tubercle (*Dt*) almost obscures the tubercle proper, or crest (*Cr*). × 2.

Fig. 39. The bone shown in Fig. 38, with labelling as before, viewed from distally. × 2.

Fig. 40. The cast of the right Olduvai trapezium (OH7) viewed from dorsally. The dorsal tubercle (*Dt*) is clearly apparent. × 3.

Fig. 41. The bone shown in Fig. 40, viewed from distally. The dorsal tubercle (*Dt*) is obvious but the tubercle proper, or crest, has been broken off, although the fractured surface (*Cr*) is clearly identifiable. × 3.
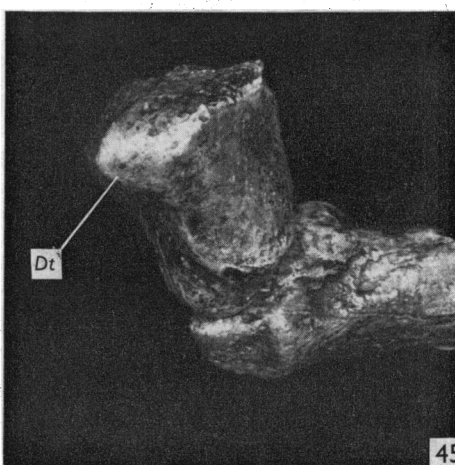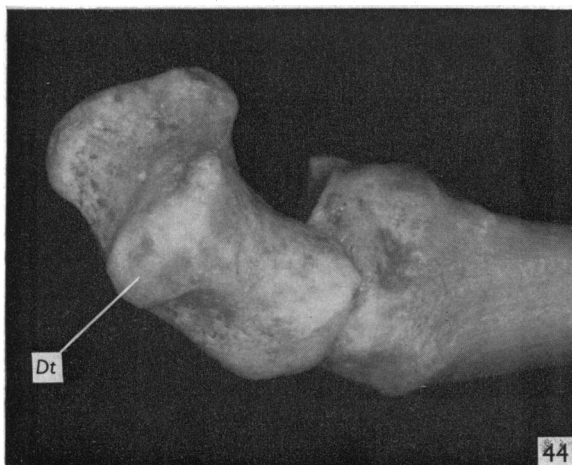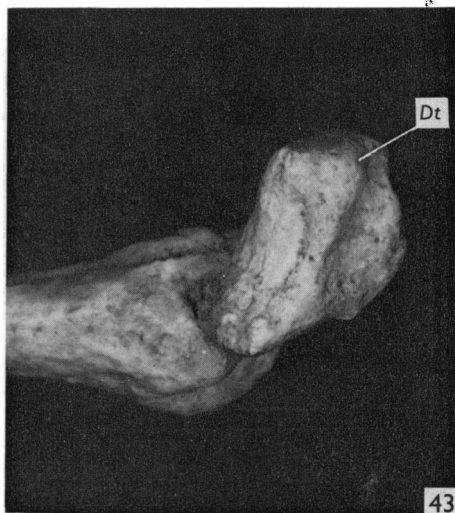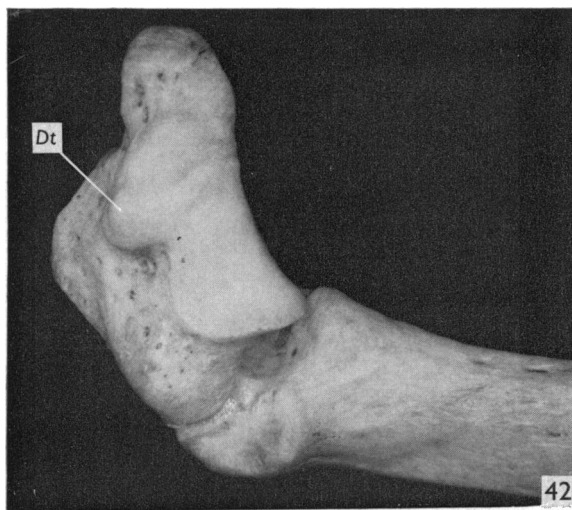
Figs. 42–45. The trapezium and second metacarpal articulated together and viewed from laterally. *Dt*, dorsal tubercle of trapezium.

Fig. 42. The bones of the right hand of *Pan troglodytes* (B.M. 1948.10.25.2). × 2.

Fig. 43. The casts of the fossil bones of the left hand of *Dryopithecus (Proconsul) africanus*. × 3.

Fig. 44. The bones of the right hand of *Homo sapiens*. × 2.

Fig. 45. The casts of the fossil bones from Olduvai (OH7). × 2.

Following this type of reasoning, Napier (1962, 1964) concluded that the Olduvai hand, with its apparent rather pongid-like 'set' of the trapezium, was capable of a strong power grip but lacked perfection of a precision grip, because the ape-like 'set' of the trapezium was said to indicate an ape-like proportionality between thumb and index finger; why this latter should follow is not obvious.

In fact, none of the bones from the ulnar side of the fossil hand is known, and the presence or absence of the unique human attributes for a power grip are similarly

unknown. However, the orientation of the trapezium indicates that the factors which fit the thumb for its role in the power grip were certainly not fully acquired.

The implication often seems to be that the precision grip represents a sort of pinnacle of locomotor achievement, and this is suggested by the term itself. In fact, it is just the grip used for small and fragile objects, and the morphological specializations associated with the human power grip are at least as great, if not greater.

CONCLUSIONS

It is a frustrating fact for students of early hominid evolution that a complete set of fossil hand bones could not be assembled even by pooling the finds from various sites with differing time horizons (often inadequately dated) and representing populations differing in specific and possibly generic rank. In the light of the foregoing observations, however, a tentative view can be formulated for the level of attainment of hand evolution at the Plio-Pleistocene boundary and during the early Pleistocene.

Dating the South African hominid sites has always been unsatisfactory and controversy has been heightened recently. Partridge (1973) has attempted to date these sites on the basis of cave-opening related to rates of nick-point migration and has arrived at approximate ages of 3·3 Myr for Sterkfontein and 2·6 Myr for Swartkrans; Tobias (1973) has accepted dates corresponding at least roughly to these on the basis of faunal comparisons. Data on fossil Bovidae (Vrba, 1975) similarly indicate that the Sterkfontein site is considerably older than Swartkrans, though perhaps the absolute dates could be as much as 1 Myr younger than those based on geomorphology; these studies further suggest that Kromdraai is much younger – about 0·5 Myr. Stone tools are known from the Swartkrans site (Leakey, 1970) and a single artefact from the Kromdraai site (Brain, 1958).

The Olduvai hominid 7 hand bones have been reliably dated at about 1·75 Myr and were associated with stone tools of the Oldowan culture (Leakey, 1971).

Tools have also been found at Lake Rudolf, Kenya, dated at 2·6 Myr (Brock & Isaac, 1974) and in the Omo valley dated at approximately 2 Myr (Merrick, De Heinzelin, Haessaerts & Howell, 1973).

Thus, the time span which has yielded the various fossil hand bones of emergent hominids has also yielded stone artefacts. The striking point about all the fossils is their essential primitiveness – their retention of many ape-like characters and the lack of those functional markers which distinguish the human hand. This applies even to the Olduvai hand bones, although they may be rather more advanced than those from South Africa; even this must be something of an open question, since the bones which might have yielded more information are lacking.

The most parsimonious hypothesis at present would seem to be that the earliest stone tools were fashioned by hands which were still lacking in those specializations distinguishing modern human hands. This also may turn out to be untrue for the issue is complicated by the evident existence at several of the sites of more than one hominid species (Blumenberg & Todd, 1974) – hand bones of the more advanced type simply may not have been found.

It is evident that many of the oft-quoted statements on early hominid hand function have been based on quite inadequate background data and represent little more

than intuitive hunches. The common practice of comparing a fossil with a series of modern primate bones, as though they were so many pottery sherds, is potentially quite misleading, and examples of the possible pitfalls are apparent from this paper. There is an obvious continuing need for more detailed functional anatomical studies, which alone can provide a sound basis for reasoned evolutionary assessments.

SUMMARY

A functional morphological study has been made of the joints of the primate hand, particular emphasis being placed upon the carpometacarpal and metacarpophalangeal joints.

The presumptive evolutionary history of these joints has been charted by reference to a comparative series of mammals.

It has been demonstrated that the human joints have been quite strikingly modified in a number of ways, and that these evolutionary changes may be logically correlated with the refined functional attributes of the human hand.

The morphological background thus established has been applied in a preliminary study of the hand bones of various fossil hominids.

REFERENCES

BARNETT, C. H. (1954). The structure and function of fibrocartilages within vertebrate joints. *Journal of Anatomy* **88**, 363–368.

BIEGERT, J. (1971). Dermatoglyphics in the chimpanzee. In *The Chimpanzee*, vol. 4 (ed. G. H. Bourne), pp. 273–324. Basel: Karger.

BISHOP, A. (1964). Use of the hand in lower Primates. In *Evolutionary and Genetic Biology of Primates*, vol. 2 (ed. J. Buettner-Janusch), ch. 12, pp. 132–225. New York: Academic Press.

BLUMENBERG, B. & TODD, N. B. (1974). On the association between *Homo* and *Australopithecus*. *Current Anthropology* **15**, 386–388.

BRAIN, C. K. (1958). *The Transvaal ape-man-bearing cave deposits. Transvaal Museum Memoir No. 11*. Pretoria: Transvaal Museum.

BROCK, A. & ISAAC, G. L. (1974). Paleomagnetic stratigraphy and chronology of hominid-bearing sediments east of Lake Rudolf, Kenya. *Nature* **247**, 344–348.

BROOM, R. (1942). The hand of the ape-man *Paranthropus robustus*. *Nature* **149**, 513–514.

BROOM, R. & ROBINSON, J. T. (1949a). A new type of fossil baboon, *Gorgopithecus major*. *Proceedings of the Zoological Society of London* **119**, 378–386.

BROOM, R. & ROBINSON, J. T. (1949b). Thumb of the Swartkrans ape-man. *Nature* **164**, 841–842.

BROOM, R. & SCHEPERS, G. W. H. (1946). *The South African fossil Ape-men: The Australopithecinae. Transvaal Museum Memoir No. 2*. Pretoria: Transvaal Museum.

CARTMILL, M. (1974). Pads and claws in arboreal locomotion. In *Primate Locomotion* (ed. Farish A. Jenkins), ch. 2, pp. 45–76. New York: Academic Press.

CLARK, W. E. LE GROS (1947). Observations on the anatomy of the fossil Australopithecinae. *Journal of Anatomy* **81**, 300–333.

CLARK, W. E. LE GROS (1967). *Man-apes or Ape-men. The Story of Discoveries in Africa*. New York: Holt, Rinehart and Winston, Inc.

DAY, M. H. & SCHEUER, J. L. (1973). SKW14147: a new hominid metacarpal from Swartkrans. *Journal of Human Evolution* **2**, 429–438.

ERIKSON, G. E. (1963). Brachiation in new world monkeys and in anthropoid apes. *Symposia of the Zoological Society of London No. 10* (ed. J. Napier and N. A. Barnicot), pp. 135–164.

ETTER, H. F. (1973). Terrestrial adaptations in the hands of the Cercopithecinae. *Folia primatologica* **20**, 331–350.

FICK, R. (1904). *Handbuch der Anatomie und Mechanik der Gelenke*. Erster Teil: *Anatomie der Gelenke*. Jena: Gustav Fischer.

FICK, R. (1911). *Handbuch der Anatomie und Mechanik der Gelenke*. Dritter Teil: *Spezielle Gelenk- und Muskel-mechanik*. Jena: Gustav Fischer.

FRAZER, J. E. (1946). *The Anatomy of the Human Skeleton*. London: Churchill.

FREEDMAN, L. (1957). The fossil Cercopithecoidea of South Africa. *Annals of the Transvaal Museum* **23**, 121–262.

GAD, P. (1967). The anatomy of the volar part of the capsules of the finger joints. *Journal of Bone and Joint Surgery* **49B**, 362–367.

GREGORY, W. K. (1934). *Man's Place among the Anthropoids*. Oxford: Clarendon Press.

HAINES, R. W. (1944). The mechanism of rotation at the first carpo-metacarpal joint. *Journal of Anatomy* **78**, 44–46.

HAINES, R. W. (1958). Arboreal or terrestrial ancestry of the placental mammals. *Quarterly Review of Biology* **33**, 1–23.

JONES, F. WOOD (1949). *The Principles of Anatomy as seen in the Hand*. London: Baillière, Tindall and Cox.

JOSEPH, J. (1951). Further studies of the metacarpophalangeal and interphalangeal joints of the thumb. *Journal of Anatomy* **85**, 221–229.

JOUFFROY, F. K. & LESSERTISSEUR, J. (1959). La main des Lemuriens Malgache comparée a celle des autres Primates. *Mémoires de l'Institut Scientifique de Madagascar* **13A**, 195–219.

KAPANDJI, I. A. (1966). *Physiologie Articulaire*. Fascicule Premier. Paris: Librairie Maloine.

KAUER, J. M. G. (1974). The interdependence of carpal articulation chains. *Acta anatomica* **88**, 481–501.

KIRK, T. S. (1924). Some points in the mechanism of the human hand. *Journal of Anatomy* **58**, 228–230.

KUCZYNSKI, K. (1974). Carpometacarpal joint of the human thumb. *Journal of Anatomy* **118**, 119–126.

LANDSMEER, J. M. F. (1955). Anatomical and functional investigations of the articulation of the human fingers. *Acta anatomica* Supplementum 24–2 ad **25**, 1–69.

LANDSMEER, J. M. F. & ANSINGH, H. R. (1957). X-ray observations on rotation of the fingers in the metacarpo-phalangeal joints. *Acta anatomica* **30**, 404–410.

LEAKEY, M. D. (1970). Stone artefacts from Swartkrans. *Nature* **225**, 1222–1225.

LEAKEY, M. D. (1971). *Olduvai Gorge. Volume 3: Excavations in Beds I and II*, 1960–1963. Cambridge: University Press.

LEWIS, O. J. (1965). The evolution of the mm. interossei in the primate hand. *Anatomical Record* **153**, 275–288.

LEWIS, O. J. (1972a). Osteological features characterizing the wrists of monkeys and apes, with a reconsideration of this region in *Dryopithecus (Proconsul) africanus*. *American Journal of Physical Anthropology* **36**, 45–58.

LEWIS, O. J. (1972b). The evolution of the hallucial tarsometatarsal joint in the Anthropoidea. *American Journal of Physical Anthropology* **37**, 13–34.

LEWIS, O. J. (1973). The hominoid os capitatum with special reference to the fossil bones from Sterkfontein and Olduvai Gorge. *Journal of Human Evolution* **2**, 1–11.

LEWIS, O. J. (1974). The wrist articulations of the Anthropoidea. In *Primate Locomotion* (ed. Farish A. Jenkins) ch. 5, pp. 143–169. New York: Academic Press.

LORENZ, R. (1974). On the thumb of the Hylobatidae. In *Gibbon and Siamang*, vol. 3 (ed. D. M. Rumbaugh), pp. 157–175. Basel: Karger.

MACCONAILL, M. A. (1941). The mechanical anatomy of the carpus and its bearing on some surgical problems. *Journal of Anatomy* **75**, 166–175.

MACCONAILL, M. A. (1953). The movements of bones and joints. The significance of shape. *Journal of Bone and Joint Surgery* **35B**, 290–297.

MACCONAILL, M. A. & BASMAJIAN, J. V. (1969). *Muscles and Movements. A Basis for Kinesiology*. Baltimore: Williams and Wilkins.

MCMASTER, M. (1972). A natural history of the rheumatoid metacarpo-phalangeal joint. *Journal of Bone and Joint Surgery* **54**, 687–697.

MERRICK, H. V., DE HEINZELIN, J., HAESSAERTS, P. & HOWELL, F. C. (1973). Archaeological occurrence of early Pleistocene age from the Shungura Formation, Lower Omo Valley, Ethiopia. *Nature* **242**, 572–575.

NAPIER, J. R. (1955). The form and function of the carpo-metacarpal joint of the thumb. *Journal of Anatomy* **89**, 362–369.

NAPIER, J. R. (1956). The prehensile movements of the human hand. *Journal of Bone and Joint Surgery* **38B**, 902–913.

NAPIER, J. R. (1959). Fossil metacarpals from Swartkrans. *Fossil Mammals of Africa, No. 17*. London: British Museum (Natural History).

NAPIER, J. R. (1960). Studies of the hands of living primates. *Proceedings of the Zoological Society of London* **134**, 647–657.

NAPIER, J. R. (1961). Prehensility and opposability in the hands of primates. *Symposia of the Zoological Society of London* **5**, 115–132.

NAPIER, J. R. (1962). Fossil hand bones from Olduvai Gorge. *Nature* **196**, 409–411.

NAPIER, J. R. (1964). Locomotor functions of hominids. In *Classification and Human Evolution* (ed. S. L. Washburn), pp. 178–189. London: Methuen.

OAKLEY, K. P. (1972). Skill as a human possession. In *Perspectives on Human Evolution*, vol. 2 (ed. S. L. Washburn and P. Dolhinow), ch. 1, pp. 14–50. New York: Holt, Rinehart and Winston, Inc.

OSBORN, H. F. (1930). The discovery of tertiary man. *Nature* **125**, 53–57.

PARTRIDGE, T. C. (1973). Geomorphological dating of cave openings at Makapansgat, Sterkfontein, Swartkrans and Taung. *Nature* **246**, 75–79.

POCOCK, R. I. (1921). The external characters of the koala (*Phascolarctos*) and some related marsupials. *Proceedings of the Zoological Society of London*, pp. 591–607.

POCOCK, R. I. (1925). Additional notes on the external characters of some platyrrhine monkeys. *Proceedings of the Zoological Society of London*, pp. 27–47.

POIRIER, P. & CHARPY, A. (1911). *Traité d'Anatomie Humaine*. Tome Premier. Paris: Masson et Cie.

PREUSCHOFT, H. (1973a). Body posture and locomotion in some East African miocene Dryopithecinae. In *Human Evolution*, volume 11, *Symposia of the Society for Human Biology* (ed. M. H. Day), pp. 13–46.

PREUSCHOFT, H. (1973b). Functional anatomy of the upper extremity. In *The Chimpanzee*, vol. 6 (ed. G. H. Bourne), pp. 34–120. Basel: Karger.

RETTERER, E. & NEUVILLE, H. (1918). Des articulations métacarpo-phalangiennes de quelques singes. *Compte rendu de la Société de biologie* **81**, 960–963.

RIGHTMIRE, G. P. (1972). Multivariate analysis of an early hominid metacarpal from Swartkrans. *Science* **176**, 159–161.

ROBINSON, J. T. (1972). *Early Hominid Posture and Locomotion*. Chicago: University of Chicago Press.

ST JOHN BROOKS, H. (1886). On the morphology of the intrinsic muscles of the little finger, with some observations on the ulnar head of the short flexor of the thumb. *Journal of Anatomy* **20**, 645–661.

SINGH, I. (1959). Variations in the metacarpal bones. *Journal of Anatomy* **93**, 262–267.

SONNTAG, C. F. (1924). *The Morphology and Evolution of the Apes and Man*. London: John Bale, Sons and Danielsson.

TESTUT, L. (1904). *Traité d'Anatomie Humaine*. Tome Premier. Paris: Octave Doin.

TOBIAS, P. V. (1973). Implications of the new age estimates of the early South African hominids. *Nature* **246**, 79–83.

TUTTLE, R. (1972). Functional and evolutionary biology of hylobatid hands and feet. In *Gibbon and Siamang*, vol. 1 (ed. D. M. Rumbaugh), pp. 136–206. Basel: Karger.

TUTTLE, R. (1974). Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. *Current Anthropology* **15**, 389–398.

VAN DAM, G. (1934). On active rotation of the metacarpalia, e.g. in spreading of the fingers. *Acta radiologica* **15**, 304–309.

VRBA, E. S. (1975). Some evidence of chronology and palaeoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature* **254**, 301–304.

WEITBRECHT, J. (1742). *Syndesmologia*. St Petersburg: Academy of Sciences.

WIRTSCHAFTER, Z. T. & TSUJIMURA, J. K. (1961). The sesamoid bones in the C3H mouse. *Anatomical Record* **139**, 399–408.

WRIGHT, J. D. (1935). An analysis of movements of various bones of the carpus during movements of the thumb and wrist joint. *Journal of Anatomy* **70**, 137–142.